Osteology of *Zalmoxes shqiperorum* (Dinosauria, Ornithopoda), based on new specimens from the Upper Cretaceous of Nălaţ-Vad (Romania)

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ABSTRACT

Nălaţ-Vad is a new fossil locality discovered in 2002 in the Sănpetru Formation (Maastrichtian, Late Cretaceous) of the Haţeg Basin (Transylvania, Romania). This site has, among others, yielded the most complete skeleton that can be referred to the ornithopods dinosaur *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003, but also isolated elements belonging to both juveniles and adult individuals. This material provides new information about the anatomy of *Z. shqiperorum*, and about the inter- and intraspecific variability within *Zalmoxes*. *Zalmoxes robustus* (Nopsca, 1902) and *Z. shqiperorum* were apparently sympatric species in Transylvania by latest Cretaceous time. The co-existence in the same locality of two closely-related species is not an isolated case among ornithopod dinosaurs.

KEY WORDS
Dinosauria,
Ornithopoda,
Zalmoxes shqiperorum,
Upper Cretaceous,
Haţeg Basin,
sympatry.

RÉSUMÉ

Ostéologie de Zalmoxes shqiperorum *(Dinosauria, Ornithopoda), d'après de nouveaux spécimens du Crétacé supérieur de Nălaţ-Vad (Roumanie).*

Nălaţ-Vad est un nouveau site fossilifère découvert en 2002 dans la Formation de Sănpetru (Maastrichtien, Crétacé supérieur) du bassin de Haţeg (Transylvanie, Roumanie). Ce site a notamment livré le squelette le plus complet à ce jour pouvant être attribué au dinosaure ornithopode *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003, mais également des ossements isolés appartenant à des individus juvéniles et adultes. Ce matériel apporte de nouvelles informations sur l'anatomie de *Z. shqiperorum*, mais également sur la variabilité inter- et intraspécifique au sein même du genre *Zalmoxes*. *Zalmoxes robustus* (Nopsca, 1902) et *Z. shqiperorum* étaient apparemment des espèces sympatriques en Transylvanie au Crétacé supérieur. La coexistence dans une même localité de deux espèces proches n'est pas un cas isolé chez les dinosaures ornithopodes.

MOTS CLÉS
Dinosauria,
Ornithopoda,
Zalmoxes shqiperorum,
Crétacé supérieur,
bassin de Haţeg,
sympatrie.

INTRODUCTION

Although Rhabdodontidae probably comprises the most abundant dinosaurs from the Upper Cretaceous of Europe, these medium-sized ornithopods remained poorly understood until recently. *Rhabdodon priscus* Matheron, 1869 was described from fragmentary material discovered in the lower Maastrichtian of La Nerthe (Bouches-du-Rhône, France). Additional material from different localities in southern France, referred to as *R. priscus*, was described later by Lapparent (1947), Garcia *et al.* (1999), Pincemaille-Quillévéré (2002), and Pincemaille-Quillévéré *et al.* (2006). Buffetaut & Le Loeuff (1991) described *Rhabdodon septimanicus* from a dentary discovered in the Campano-Maastrichtian of Montmouliers (Hérault, France). *Rhabdodon* Matheron, 1869 specimens have also been described in different Campano-Maastrichtian localities from northern Spain (Pereda-Suberbiola & Sanz 1999). Bunzel (1871) described *Iguanodon suessi* from the Upper Cretaceous of Niederösterreich (Austria). Seeley (1881) subsequently created the genus *Mochlodon* to include this species. In the beginning of the 20th century, Nopcsa described important ornithopod material from the Upper Cretaceous of the Haţeg Basin in Transylvania. Part of this material was referred to *Mochlodon suessi* Seeley, 1881 and another part to a new species *Mochlodon robustum* Nopcsa, 1902 (Nopcsa 1902, 1904). He later suggested that *Mochlodon* might be identical to *Rhabdodon* and that sexual dimorphism might be responsible for the observed differences between the two forms (Nopcsa 1915, 1929). Ösi (2004) reported rhabdodontid fossils in the Upper Cretaceous of Hungary. Weishampel *et al.* (2003) recently reviewed the rhabdodontid material from Transylvania, and referred it to as a new genus, *Zalmoxes*. They distinguished two species: *Z. robustus* (Nopcsa, 1902), known from abundant skull and postcranial material, and the more poorly known species *Z. shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003. Both species are known from several localities in the Haţeg Basin, but also from the Vintu de Jos area (Fig. 1). The holotype of *Z. shqiperorum* (BMNH R4900) is a single incomplete adult individual. Much of the referred material pertains to a partially associated skeleton of a juvenile, which includes most of the pelvis and associated dorsal, sacral and caudal vertebrae (FGGUB R1087-1133 and R1355-1357). From the skull of *Z. shqiperorum*, only the dentary is known to date. Both the fore- and hindlimbs were also incompletely known. Sachs & Hornung (2006) referred specimens discovered in Austria to *Zalmoxes.*

New material that can be referred to as *Z. shqiperorum* was discovered in 2002 at Nălaţ-Vad, a new locality in the Sănpetru Formation of the Haţeg Basin. The new material, housed in the Catedra de Geologie, Facultatea de Biologie şi Geologie, Universitatea din Babes-Bolyai (Cluj-Napoca, Romania), includes the most complete skeleton that can be referred to date to this taxon (UBB NVZ1), but also isolated elements belonging to both juvenile and adult individuals. It provides new information about the anatomy of *Z. shqiperorum*, and about the inter- and intraspecific variability within *Zalmoxes*.

The aim of the present paper is to complete the osteological description of *Z. shqiperorum*, whose skeleton is scarcely known so far, on the basis of the newly-discovered material from Nălaţ-Vad. The diagnoses of both *Zalmoxes* and *Z. shqiperorum* and the apparent sympatry of two closely-related species of medium-sized herbivorous dinosaurs will be discussed.

ABBREVIATIONS

BMNH	Department of Palaeontology, Natural History Museum, London;
FGGUB	Facultatea de Geologie şi Geofizics, Universitatea din Bucareşti;
UBB	Catedra de Geologie, Facultatea de Biologie şi Geologie, Universitatea din Babes-Bolyai, Cluj-Napoca.

GEOLOGICAL SETTING

The Nălaţ-Vad locality is a newly discovered exposure situated in the bedding of the Raul Mare River between the villages of Nălaţ and Vad. Usually, the water flow covers nearly the entire exposure, so that the excavation conditions are particularly hard. The strike of the layers (N40E75N) does not significantly differs from the strike of the Toteşti-Baraj locality (Codrea *et al.* 2002), situated 3 km upstream. According to the geological map of the area, the outcropping sediments belong to the Sănpetru Formation (Grigorescu 1983, 1992; Grigorescu *et al.* 1999; Van Itterbeeck *et al.* 2004). Palaeomagnetic studies suggest that this formation should entirely belong to the lower Maastrichtian (Panaiotu & Panaiotu 2002). The facies assemblage at Nălaţ-Vad indicates a fluvial palaeoenvironment with sandy channel infills and dominantly black to reddish-brown overbank fines. The overbank fines are dominantly silts and clays representing suspension deposits on the ancient floodplain.

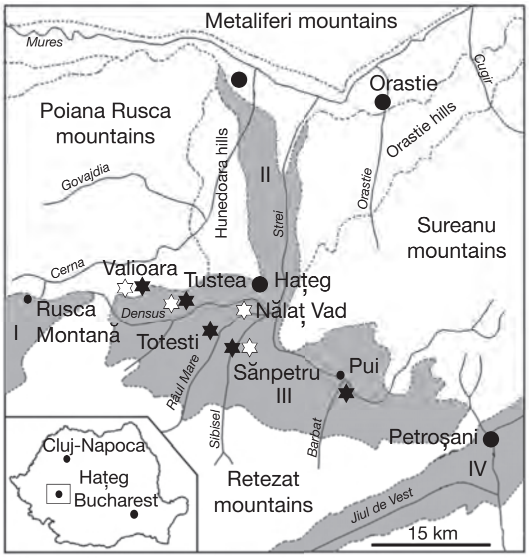

FIG. 1. — Geographical location of the different localities that have yielded fossils of *Zalmoxes robustus* (Nopsca, 1902) (black stars) and *Z. shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 (white stars) in Haţeg and surrounding basins (Romania): **I**, Rusca Montană Basin; **II**, Strei Basin; **III**, Haţeg Basin; **IV**, Petroşani Basin.

Numerous palaeosols developed within these deposits, as indicated by the presence of calcretes and the reddish coloration of the sediments (Smith *et al.* 2002; Van Itterbeeck *et al.* 2004). Dinosaur eggs were found in these calcretes, but they are less numerous than at Toteşti-Baraj. On the other hand, vertebrate remains are by far more numerous at Nălaţ-Vad. Although isolated bones were randomly found in the entire locality, three pockets have yielded concentrated vertebrate remains. A pocket with microvertebrates consists of a limestone mainly composed of eggshell debris, a so-called *coquina* that grades into black-coloured marls that is less enriched in egg shells. Both the marl and limestones are extremely rich in microvertebrate remains, mainly mammals, birds and small theropods. The second pocket was rich in sauropod bones. The third pocket has yielded disarticulated *Zalmoxes* bones, apparently belonging to a single individual (UBB NVZ1). However, one slender quadrate from this pocket apparently does not belong to *Zalmoxes*, more closely resembling that of the more advanced iguanodontian *Telmatosaurus* Nopcsa, 1903.

SYSTEMATIC PALAEONTOLOGY

Order ORNITHISCHIA Seeley, 1887
Suborder ORNITHOPODA Marsh, 1881
EUORNITHOPODA
(*sensu* Weishampel 1990)
Infraorder IGUANODONTIA Sereno, 1986
Family RHABDODONTIDAE
Weishampel, Jianu, Cziki & Norman, 2003

Genus *Zalmoxes*
Weishampel, Jianu, Cziki & Norman, 2003

TYPE SPECIES. — *Zalmoxes robustus* (Nopcsa, 1902) by original designation.

EMENDED DIAGNOSIS. — Unambiguous synapomorphies of the genus include the following characters: reduced external mandibular fenestra positioned anteriorly along the upper border of the surangular; well-developed supra-acetabular process on the ilium; absence of an obturator process on the ischium; arched ischial shaft.

The following characters may be synapomorphic for *Z. robustus* and *Z. shqiperorum*, but their presence in *Rhabdodon* remains unknown (see discussion): extensive, complex squamose suture between quadratojugal and jugal; post-temporal foramen transmitted through the body of the squamosal; curved shelf on the lateral surface of the postorbital; lateral splaying of the quadrate; deep predentary; long, dorsoventrally-narrow, twisted preacetabular process.

The following characters cannot be observed either in *Z. shqiperorum* or in the different species of *Rhabdodon*. Therefore, subsequent discoveries may shift their distribution either inclusively (as synapomorphies for the Rhabdodontidae clade) or exclusively (as autapomorphies for *Z. robustus*): absence of the scar for *m. adductor mandibulae externus superficialis* on the squamosal; large, disc-shaped quadratojugal; frontal with complex transverse sutural surface that extensively overlaps the parietal; high lateroventral processes on the predentary.

Zalmoxes shqiperorum
Weishampel, Jianu, Cziki & Norman, 2003

HOLOTYPE. — BMNH R.4900, left dentary, sacrum, right scapula, right coracoid, partial ?left ilium, partial right ilium, right ischium, left distal ischium and left femur.

EMENDED DIAGNOSIS. — Species of *Zalmoxes* characterised by the following autapomorphies: occipital condyle not separated from the sphenooccipital tubercles (= basal tubera) by a distinct neck; dentary with an angular buccal emargination that forms a horizontal platform extending for the full length of the dentition behind and medial to the coronoid process; scapular blade narrow, strap-like proximally, expanding sharply posterodistally; expanded region of the scapula adjacent to the coracoid suture; acromial process forming a prominent flange; deltopectoral crest of the humerus particularly prominent, extending over the proximal half of the humerus; iliac peduncle of the ischium particularly developed; distal end of the ischium forming a boot-like expansion.

DESCRIPTION OF THE *ZALMOXES* MATERIAL FROM NĂLAŢ-VAD

This description is mainly based on UBB NVZ1, the disconnected skeleton discovered in the third fossiliferous pocket at Nălaţ-Vad. Approximately 70% of the skull is known from disarticulated bones in this specimen. A tentative reconstruction of the skull of UBB NVZ1 is presented in Figure 2A, B. The axial skeleton, the pes and the manus are very incompletely preserved in UBB NVZ1. Therefore, the description of the postcranium is completed by information observed on isolated bones collected in other places of the Nălaţ-Vad locality. A reconstruction of the whole skeleton of *Z. shqiperorum* (with the exception of the pes and the manus) is presented in Figure 2C.

Jugal (Fig. 3) (UBB NVZ1-32)

The jugal of *Z. shqiperorum* is more gracile than that of *Z. robustus* (see Weishampel *et al.* 2003: fig. 6A, B). The dorsal border of the long maxillary process forms a very wide platform-like ventral orbital rim (Fig. 3B). The lateral surface of the maxillary process bears an elongated groove (Fig. 3A). Quite anteriorly, the external side of the maxillary process forms a small but deep recess for articulation with the posteroventral corner of the lacrimal. The medial side of the jugal forms a very elongated and deep recess for articulation with the posterior part of the maxilla. At the level of the posteroventral corner of the orbit, the medial side of the maxillary process bears a wide grooved and ridged facet for intimate articulation with the ectopterygoid (Fig. 3C). The posterior process is very compressed mediolaterally. Its ventral border is sigmoid, thickened and covered with longitudinal striations, indicating fibrous attachment of the superficial tissues associated with

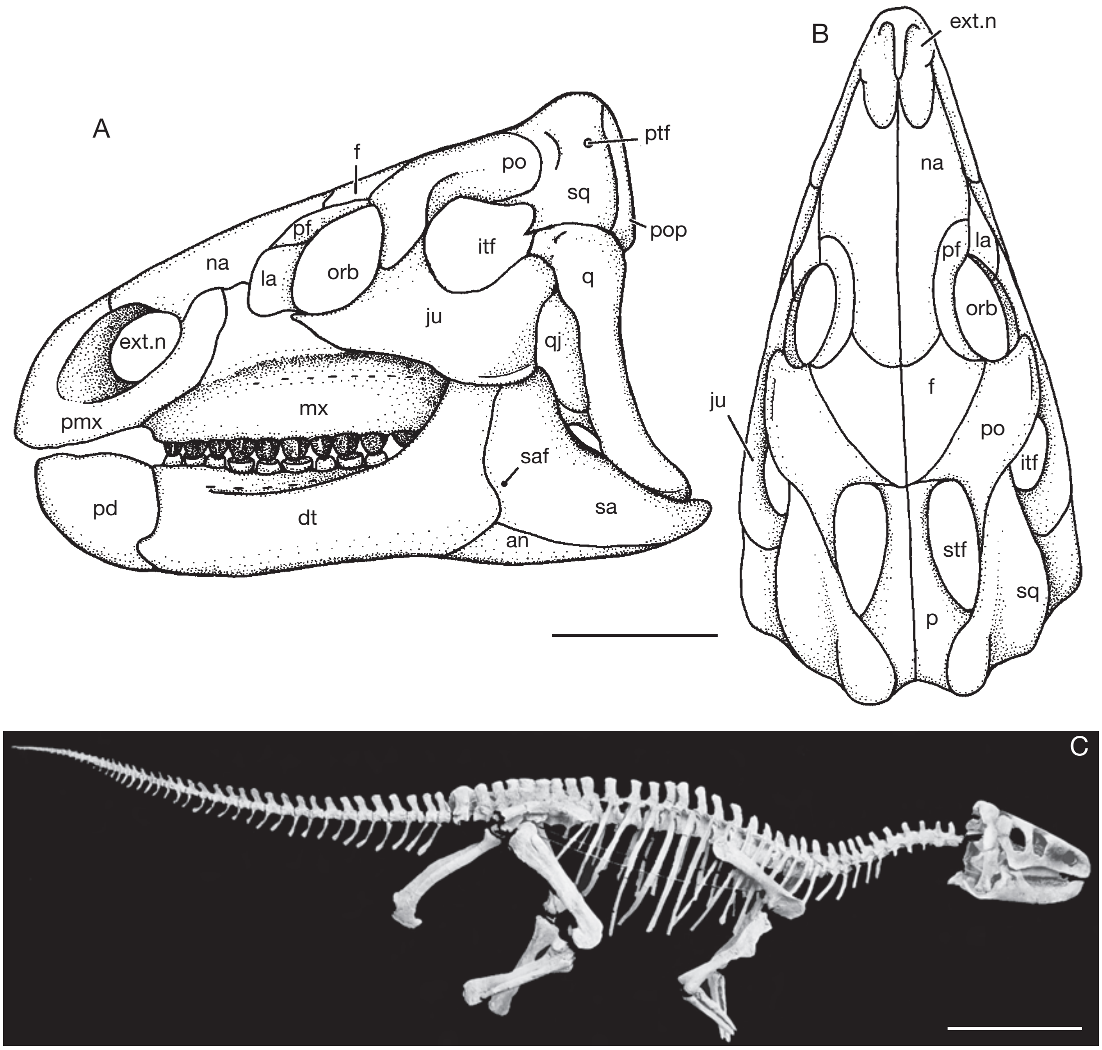

Fig. 2. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003, skull reconstruction in left lateral (**A**) and dorsal (**B**) views; skeletal reconstruction (except the hands and the feet) in right lateral view (**C**). Abbreviations: **an**, angular; **dt**, dentary; **ext.n**, external naris; **f**, frontal; **itf**, infratemporal fenestra; **ju**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **orb**, orbital cavity; **p**, parietal; **pd**, predentary; **pf**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pop**, paroccipital process; **ptf**, post-temporal fenestra; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **saf**, surangular fenestra; **sq**, squamosal; **stf**, supratemporal fenestra. Scale bars: A, B, 5 cm; C, 20 cm.

the cheek region. On the medial side of the posterior process, a prominent vertical ridge limits a wide articular facet for the quadratojugal (Fig. 3C). The posterior edge of the jugal is ventrally notched and forms a slot that received the anterior edge of the quadratojugal. This complex articulation between the jugal and quadratojugal was previously described by Weishampel *et al.* (2003) in *Z. robustus*. As it has not yet been observed in any other ornithopod known to date, it can be considered as diagnostic for *Zalmoxes*. However, the jugal has not been described in *Rhabdodon* yet, thus it is also possible that this type of articulation characterizes the rhabdodontid clade.

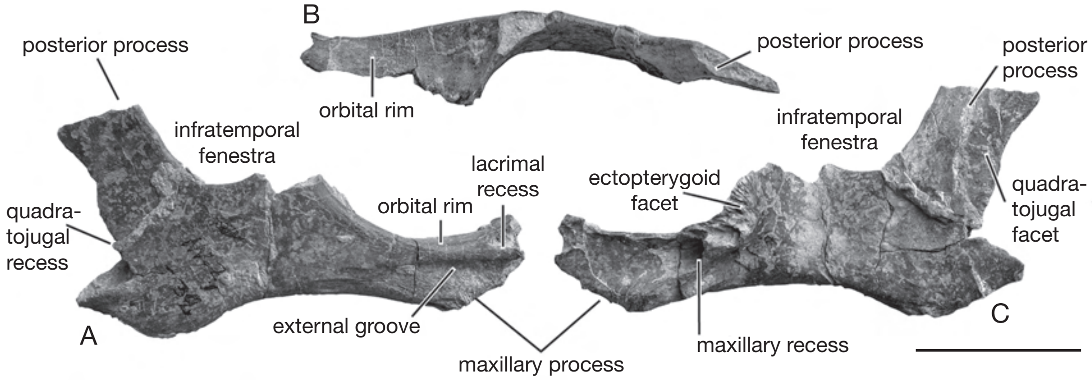

FIG. 3. — Right jugal of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 (UBB NVZ1-32), from the Upper Cretaceous of Nălaţ-Vad (Romania), in lateral (**A**), dorsal (**B**), and medial (**C**) views. Scale bar: 5 cm.

Squamosal (Fig. 4A, B) (UBB NVZ1-33)

The parietal process of the squamosal is proportionally shorter and higher than in *Z. robustus*. Its dorsal margin, which participates in the posterolateral part of the supratemporal fenestra, is particularly thick and rugose. Its medial surface bears a long horizontal ridge-bound facet, interpreted by Weishampel *et al.* (2003) as an articulation surface for the paroccipital process. A different interpretation is proposed herein. In UBB NVZ1-33, the paired squamosals and the parietal are still articulated (Fig. 4C). It is clear, from this specimen, that the ridge-bound facet on the medial side of the parietal process of the squamosal intimately contacted the posterolateral surface of the parietal instead. The parietal processes of the paired squamosals nearly contact each other along the midline on the occipital aspect of the skull, being only separated by the narrow posteroventral keel of the parietal (Fig. 4C, D).

The postorbital process of the squamosal is also more robust than in *Z. robustus*. Its lateral surface forms a wide and scarred articular facet for the postorbital (Fig. 4A). Because of the preservation state of the postorbital ramus, it cannot be checked whether a scar for the origin of *m. adductor mandibulae externus superficialis* is developed on the squamosal of *Z. shqiperorum*. The absence of this scar is regarded by Weishampel *et al.* (2003) as diagnostic for *Zalmoxes*, but the state of this character remains unknown in *Z. shqiperorum* and in *Rhabdodon* as well. The posterior margin of the infratemporal fenestra forms a large notch between the ventral border of the postorbital process and the anterior margin of the squamosal body. This notch appears lower, but deeper than in *Z. robustus* (Weishampel *et al.* 2003: fig. 9).

Ventrally, the squamosal body forms a large and deep cotylus for the head of the quadrate. As previously noted by Weishampel *et al.* (2003), the shape and orientation of the cotylus suggests an oblique orientation for the long axis of the quadrate (Fig. 4B). An anteroventrally-pointing prequadratic process limits the cotylus anteriorly. On the other hand, the postquadratic process is absent and the posteroventral corner of the squamosal curves medially instead, as previously described in *Z. robustus* (Weishampel *et al.* 2003). On the medial surface of the squamosal body, a vertical ridge starts from the dorsal margin of the cotylus. It can be interpreted as the insertion area for the *m. adductor mandibulae externus medialis*.

As in *Z. robustus*, a foramen, interpreted as the post-temporal fenestra that has migrated from a marginal position (Weishampel *et al.* 2003), perforates the body of the squamosal. In *Z. shqiperorum*, this foramen is located at mid-distance between the notch for the infratemporal fenestra and the posterior border of the squamosal body (Fig. 4A, B), whereas it is apparently positioned more posteriorly in *Z. robustus*. As this foramen is now described both in *Zalmoxes robustus* and in *Z. shqiperorum*, and has not been described in any other ornithopod

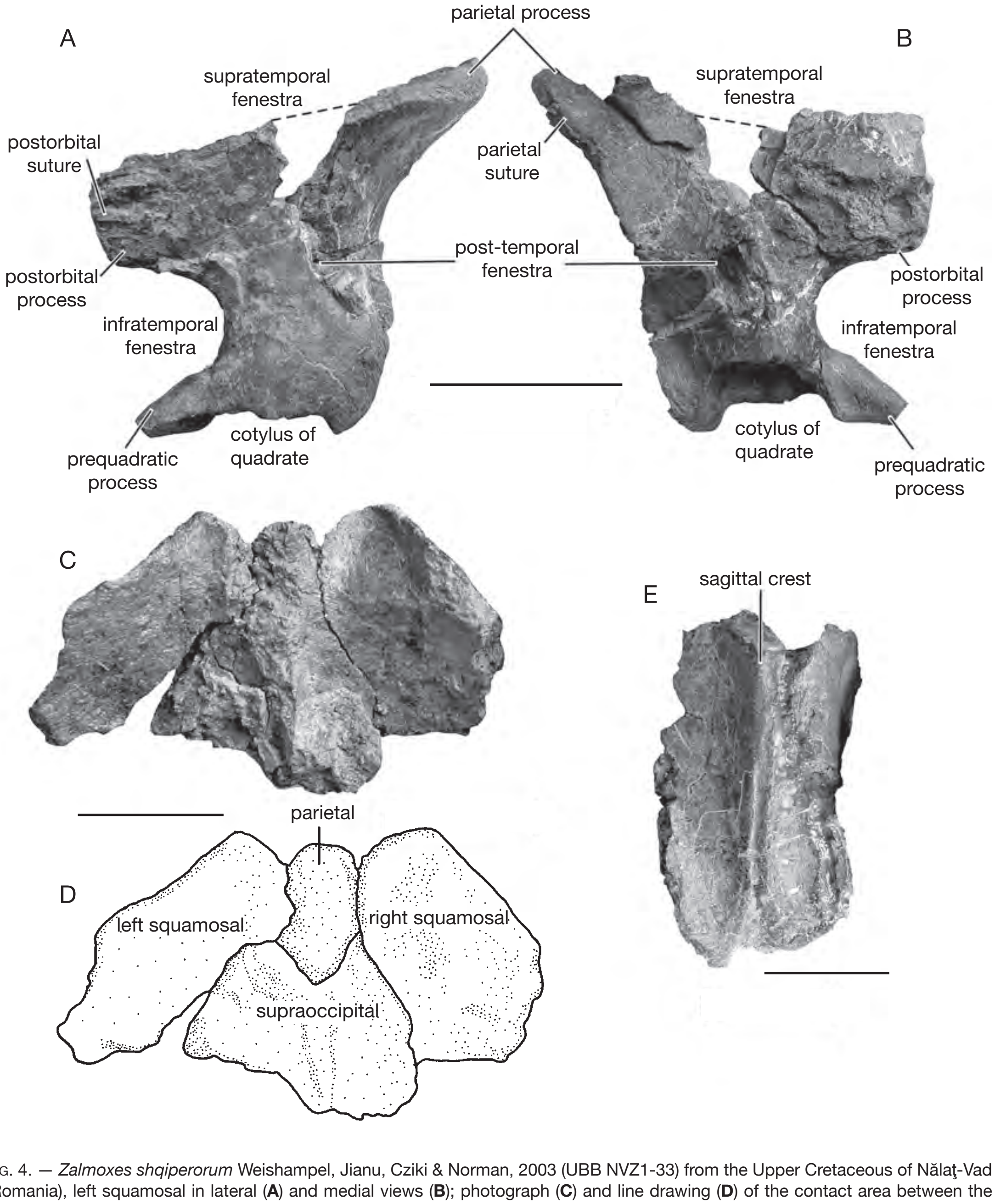

FIG. 4. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 (UBB NVZ1-33) from the Upper Cretaceous of Nălaţ-Vad (Romania), left squamosal in lateral (**A**) and medial views (**B**); photograph (**C**) and line drawing (**D**) of the contact area between the squamosals, the parietal, and the supraoccipital; parietal (**E**) in dorsal view. Scale bars: A-D, 4 cm; E, 2 cm.

known to date, it can therefore be regarded as a good synapomorphy for *Zalmoxes*. Nevertheless, it cannot be excluded that this character would be in fact synapomorphic for Rhabdodontidae (*sensu* Weishampel *et al.* 2003), because no squamosal is currently described in *Rhabdodon*.

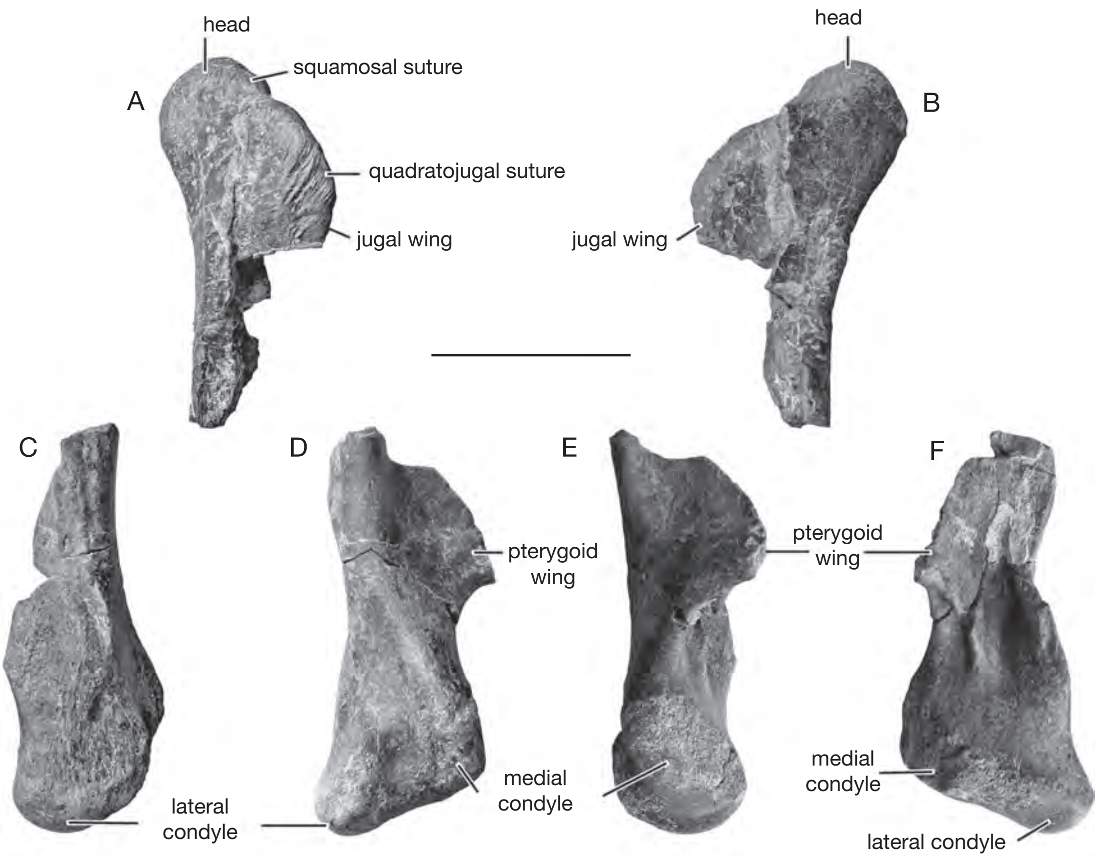

FIG. 5. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), dorsal part of right quadrate (UBB NVZ1-39) in lateral (**A**) and medial (**B**) views; dorsal part of left quadrate (UBB NVZ1-40) in lateral (**C**), posterior (**D**), medial (**E**), and anterior (**F**) views. Scale bar: 5 cm.

Quadrate (Fig. 5) (UBB NVZ1-39 and NVZ1-40)
Only the dorsal part of the right quadrate (Fig. 5A, B) and the ventral portion of the left quadrate (Fig. 5C-F) are preserved in the fossiliferous lens. The quadrate of *Z. shqiperorum* is very massive in comparison with other ornithopods, closely resembling that described in *Z. robustus* (Weishampel *et al.* 2003: fig. 7). There is no indication of a vertical buttress that posteriorly overhangs the main shaft, as it is observed in *Z. robustus* (Weishampel *et al.* 2003: fig. 7). At this level, the posterior margin of the quadrate shaft is smoothly concave (Fig. 5A, B). On the other hand, the anterolateral border of the quadrate forms a very massive jugal wing.

The ventral portion of the quadrate is asymmetrically developed into a large lateral condyle, which articulated with the surangular part of the mandibular glenoid, and a smaller medial condyle, which probably articulated with the articular part of the mandibular glenoid (Fig. 5D, F). Weishampel *et al.* (2003) showed that the important asymmetry of the ventral condyles, in association with the orientation of the squamosal cotylus, implies a strongly oblique orientation of the quadrate relative to the sagittal plane of the skull and a triangular aspect of the skull in posterior view. This character is regarded as diagnostic for *Zalmoxes*, because it is shared by both species *Z. robustus* and *Z. shqiperorum*. However, it must be noted that the important asymmetry of the distal quadrate condyles also characterises the more derived hadrosaurid clade (Weishampel *et al.* 1993; Godefroit *et al.* 1998). Although it is incompletely preserved, the pterygoid wing seems massive.

Parietal (Fig. 4E) (*UBB NVZ1-33)*
Only the posterior part of the parietal, which intimately contacts the medial side of the squamosals, is preserved in UBB NVZ1-33. As previously observed in *Z. robustus* (Weishampel *et al.* 2003), the parietal appears particularly narrow and lozenge-shaped in cross-section. Its dorsal surface bears a high and sharp sagittal crest, much better developed than in *Z. robustus* (Weishampel *et al.* 2003: fig. 10C). The height of the sagittal crest progressively lessens posteriorly, as it slightly bifurcates.

Frontal (Fig. 6) (UBB NVZ1-38)
In dorsal view, the frontal is subtriangular and it closely resembles that of *Z. robustus* (Weishampel *et al.* 2003: fig. 8B). Its anterior margin forms a broad but shallow articular surface for the nasal and, maybe, for the prefrontal.The posteromedial border of the parietal is slightly notched: the anterior end of the parietal therefore probably separated the paired frontals at this level. Because the posterior portion of the frontal is broken off, it cannot be checked whether the frontal overlapped for some extent the parietal. This character is regarded by Weishampel *et al.* (2003) as synapomorphic for *Zalmoxes*, but the state of this character remains unknown in *Z. shqiperorum* and in *Rhabdodon*. Laterally, the suture with the postorbital is also very long and thick. The relationships between the frontal and the prefrontal remain obscure. Weishampel *et al.* (2003) proposed that the anterior part of the frontal was overlapped by the posterior part of the prefrontal, close to the fronto-nasal suture. But it is also possible that the anterior part of the long and thick lateral border of the frontal contacted the prefrontal. In any case, it seems that the frontal was completely or nearly completely excluded from the orbital margin.

The ventral surface of the frontal is marked by encephalic impressions. Its posterior portion is deeply excavated by the anterior part of the cerebrum. The olfactory bulbs form elongated sulci along the interfrontal suture. Between the impressions for the cerebrum and the olfactory bulb, divergent ridges mark articulation with the sphenethmoid plate.

Postorbital (Fig. 7) (UBB NVZ1-41)
The postorbital of *Z. shqiperorum* is particularly massive. The medial border of its anterior plate is very thick and rugose for intimate contacts with the frontal. Its lateral edge, which participates in the posterodorsal margin of the orbit, is on the other hand rather sharp. The surface of the bone is not sufficiently well preserved in order to assess whether it is pierced by foramina, as it is described in *Z. robustus* (Weishampel *et al.* 2003). At the junction with the base of the squamosal process, the dorsal surface of the postorbital plate forms a well-developed curved ledge (Fig. 7B), as also observed in *Z. robustus* and interpreted by Weishampel *et al.* (2003) as marking the origin of part of the external mandibular adductor musculature. This ledge was not described in other ornithopods; it can therefore be regarded as a valid synapomorphy for *Zalmoxes*.

The squamosal process, which participates in the anterolateral margin of the supratemporal fenestra and in the dorsal margin of the infratemporal fenestra, is straight and very compressed mediolaterally. At the junction between the anterior plate, the squamosal process and the jugal process, a very depressed area marks the synovial contact with the laterosphenoid (Fig. 7C).

Supraoccipital (Fig. 4C) (UBB NVZ1-33)
The posterior surface of the supraoccipital bears a strong median nuchal crest. Transverse furrows separate this crest from lateral low bosses, which probably form the insertion areas for *m. rectus capitis posterioris*. The ventral border of the supraoccipital is notched by the dorsal margin of the foramen magnum.

Basioccipital-basisphenoid (Fig. 8) (UBB NVZ1-40)
In posterior view, the occipital condyle is wide and reniform. Its articular surface faces quite posteriorly. Its concave dorsal side participates in the floor of the foramen magnum. Contrary to *Z. robustus*, the occipital condyle is not supported

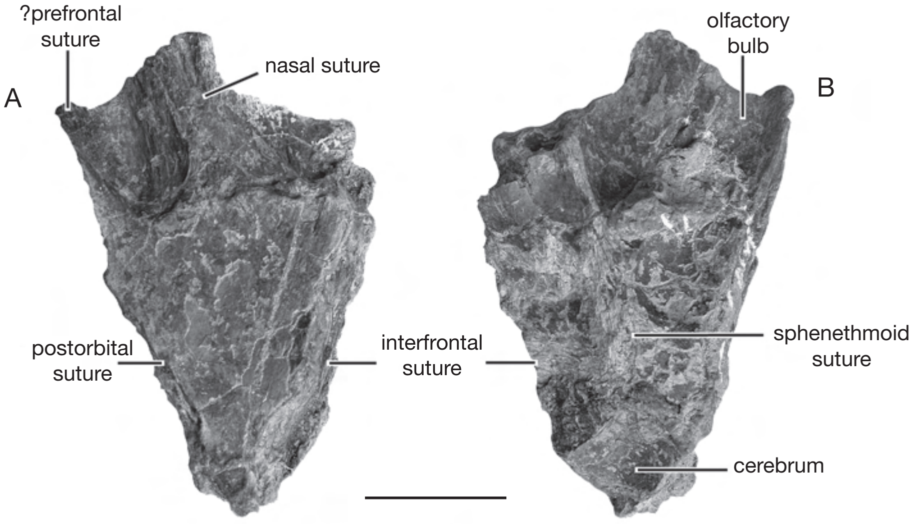

FIG. 6. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), left frontal (UBB NVZ1-38) in dorsal (**A**) and ventral (**B**) views. Scale bar: 2 cm.

by a narrower hemicylindical neck. On the other hand, the condyle is directly connected with a pair of prominent sphenoccipital tubercles, projecting lateroventrally from the basioccipital and the basisphenoid. This is the condition usually observed in hadrosaurids. It must be noted that in *Telmatosaurus* the occipital condyle is also supported by a short but distinct neck (Weishampel *et al.* 1993).

Between the sphenooccipital tubercles, the ventral side of the basioccipital-basisphenoid complex forms a deep fossa that may mark the attachment site for *m. rectus capitis anterioris* (Fig. 8A). The deep carotid canal runs obliquely between the sphenoccipital tubercles and the dorsal part of the broken basipterygoid processes (Fig. 8B). Anteriorly on the endocranial surface of the basisphenoid, the hypophyseal cavity forms a deep, but narrow depression.

Dentary (Fig. 9) (UBB NVZ1-1 and NVZ1-2)

As previously noted by Weishampel *et al.* (2003), the dentary of *Z. shqiperorum* is more massively constructed than that of *Z. robustus*. In lateral view, the ventral and dorsal borders of the dentary are parallel and regularly curved ventrally. Beneath and anterior to the coronoid process, the lateral surface of the dentary body is flat to slightly convex. It forms a distinct angle with the widely developed buccal platform, which separates the coronoid process from the dentition and extends anteriorly along the full length of the tooth row (Fig. 9A). Weishampel *et al.* (2003) regarded this important development of the buccal platform as one of the main autapomorphies for *Z. shqiperorum.* Two or three large neurovascular foramina open along the margin of the buccal platform anterior to the coronoid process.

The coronoid process is relatively stout and inclined posteriorly. It gradually rises from the marked angle between the lateral wall of the dentary body and the buccal platform. Its lateral surface is striated, reflecting the attachment of the adductor musculature. Its medial surface is in close contact with the coronoid bone, and its posterior surface with the surangular.

In dorsal view, the tooth row is straight. It contains nine tooth positions. In medial view, a robust bony parapet conceals the dentition. A curved line of alveolar foramina and interconnecting groove forms the ventral limit of the parapet (Fig. 9B). The adductor fossa is vast and extends

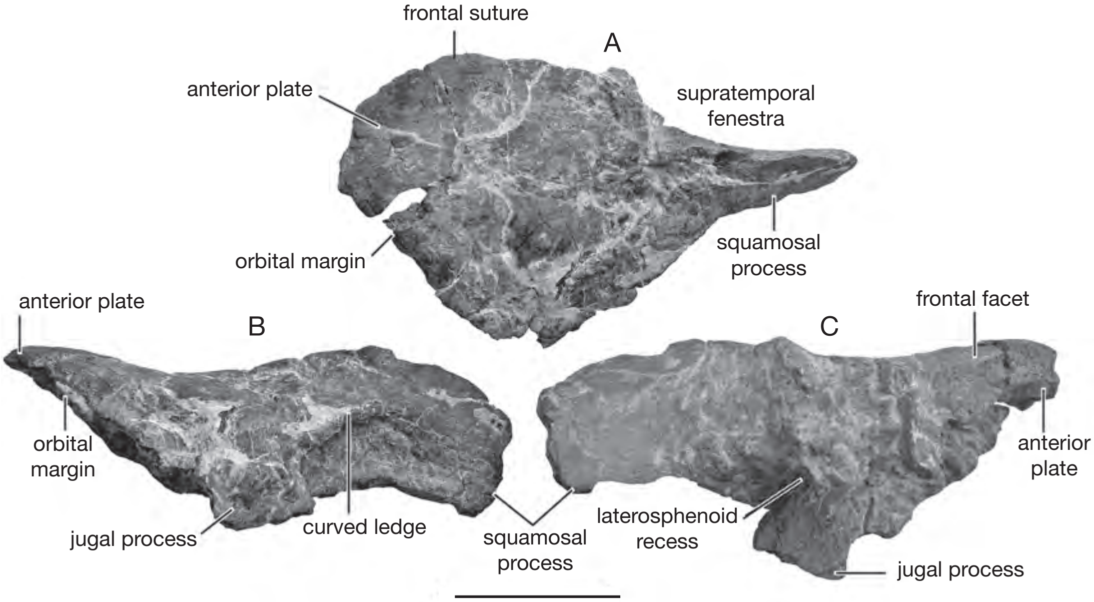

FIG. 7. — Left postorbital (UBB NVZ1-41) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania) in dorsal (**A**), lateral (**B**), and medial (**C**) views. Scale bar: 3 cm.

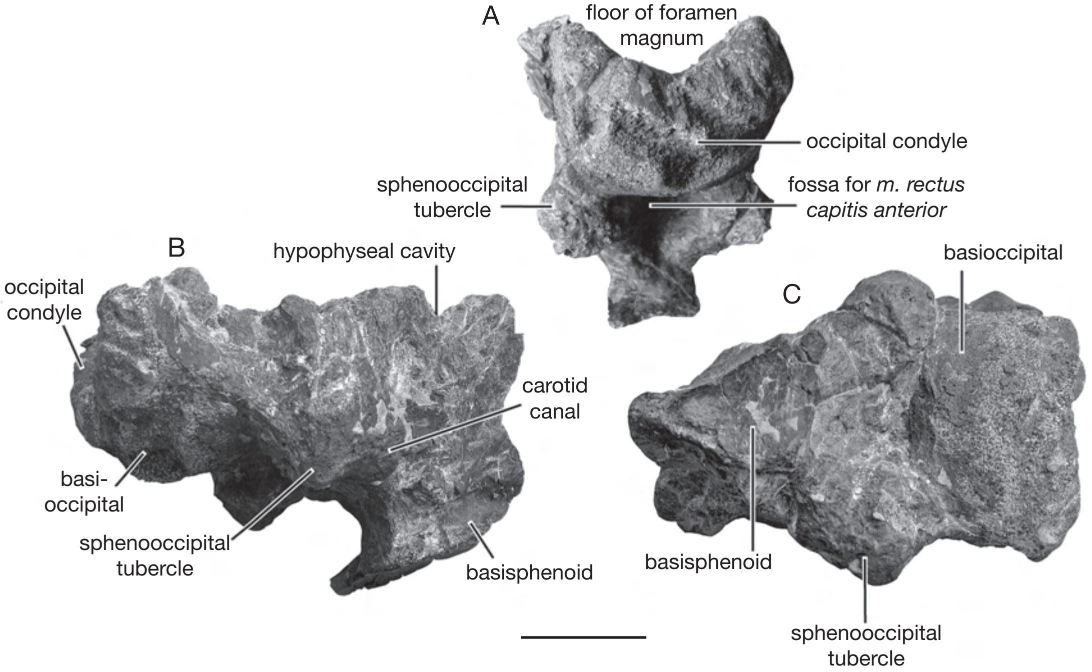

FIG. 8. — Basioccipital-basisphenoid complex (UBB NVZ1-40) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania) in posterior (**A**), right lateral (**B**), and ventral (**C**) views. Scale bar: 2 cm.

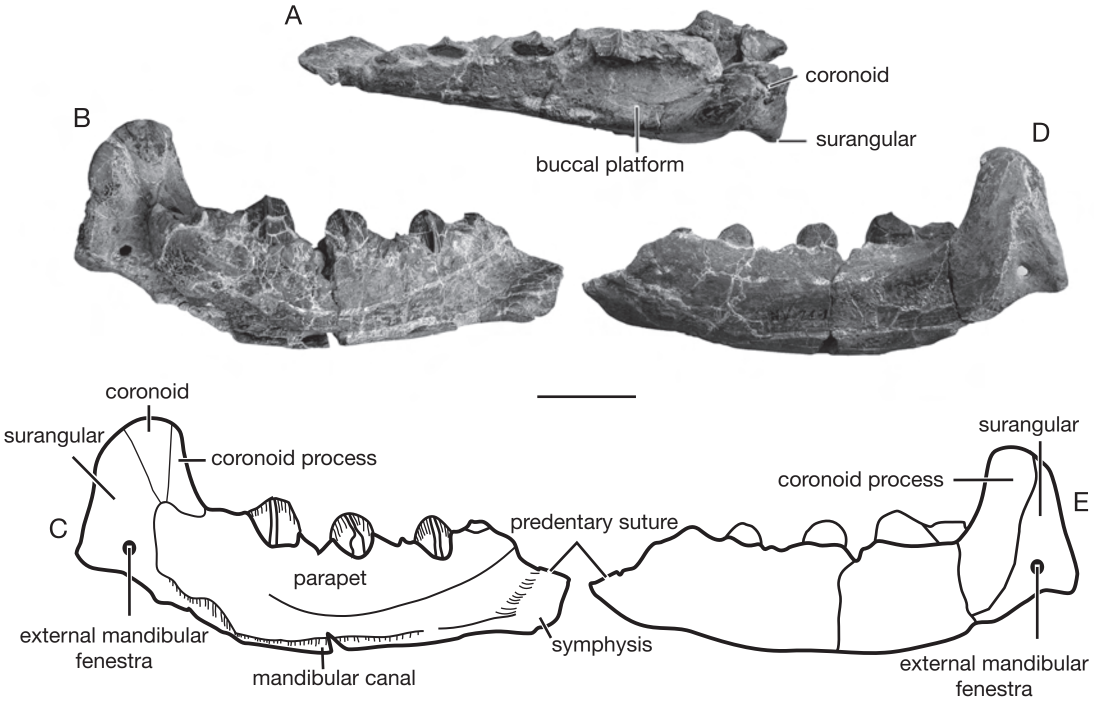

Fig. 9. — Left dentary – surangular – coronoid complex (UBB NVZ1-1) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in dorsal (**A**), medial (**B**, **C**), and lateral (**D**, **E**) views. Scale bar: 5 cm.

anteriorly as the mandibular canal nearly the length of the dentary. It terminates just posterior to the mandibular symphysis. The symphysis forms an irregular inclined surface. As is usual in ornithopods, the articular surface for the predentary forms, when the paired dentaries are articulated, a scoop-shaped surface. There is no diastema between the last dentary tooth and the articular surface for the predentary.

Coronoid (Fig. 9A, B) (UBB NVZ1-1 and NVZ1-2)
The coronoid is tightly applied along the medial aspect of the coronoid process of the dentary. The separation between both elements can be observed as a deep groove along the apex of the coronoid process (Fig. 9B).

Surangular (Fig. 9) (UBB NVZ1-1 and NVZ1-2)
The surangular is very intimately applied along the posterior side of the dentary. A small rounded foramen that opens on the dorsal part of the surangular, close to the anterior border, towards the adductor fossa, is interpreted by Weishampel *et al.* (2003) as a reduced external mandibular fenestra.

Predentary (Fig. 10) (UBB NVZ1- 35)
The predentary is very high, deep, and subtriangular in lateral view. Its anterior border forms an angle of approximately 45° to the horizontal. Numerous grooves and ridges ornament its external surface, suggesting that it was covered by a keratinous rhamphotheca in life. Unlike in *Z. robustus*, the oral margin is chisel-like, with a particularly sharp outer edge (Fig. 10B). The U-shaped posteroventral surface of the predentary, which articulated with the anterior portion of the paired dentaries, is formed by a deep and wide groove, surrounded by high lateral and medial ridges that stabilized the symphyseal region of the mandible (Fig. 10C). The high lateroventral processes, regarded by Weishampel *et al.* (2003) as diagnostic for *Zalmoxes*, are not preserved in the available material. Therefore, it cannot be decided yet whether this character is really

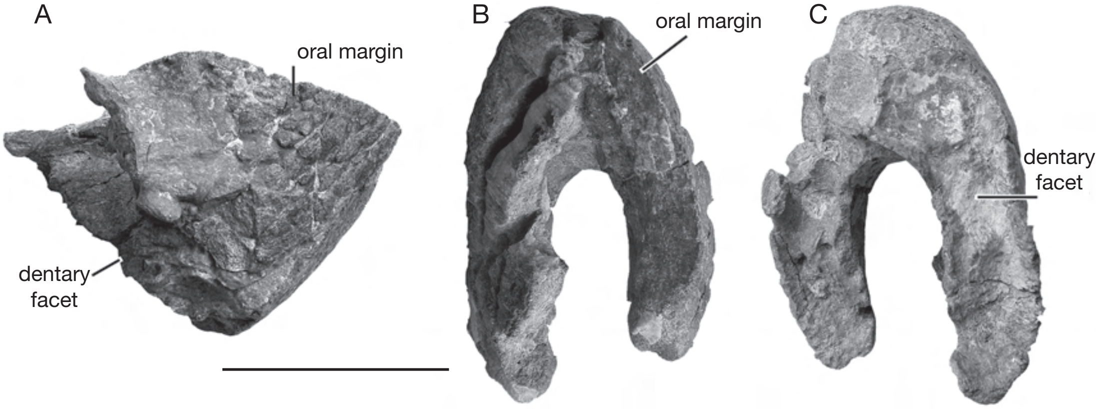

Fig. 10. — Predentary (UBB NVZ1-35) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003, from the Upper Cretaceous of Nălaţ-Vad (Romania), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. Scale bar: 4 cm.

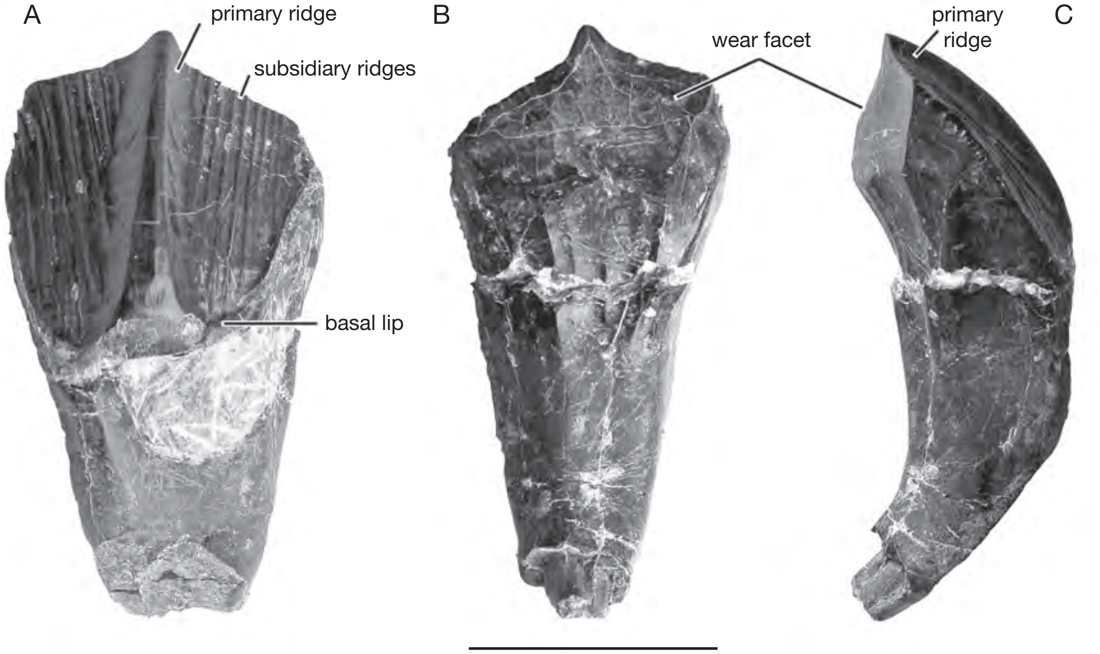

Fig. 11. — Isolated dentary tooth (UBB NVZ1-43a) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in lingual (**A**), labial (**B**), and mesial (**C**) views. Scale bar: 2 cm.

synapomorphic for both *Z. robustus* and *Z. shqiperorum*, or autapomorphic for *Z. robustus*.

Dentary teeth (Fig. 11) (UBBNVZ1-43)

The dentary teeth of *Z. shqiperorum* are particularly massive. The crown is slightly taller than wide. The enamel is distributed on both sides of the crown. The labial side is usually heavily worn (Fig. 11B). Wear begins on the distal half of the crown. A second facet develops mesially as attrition continues. The two facet merge and cannot be distinguished on heavily-worn teeth. The angle of wear ranges between 55

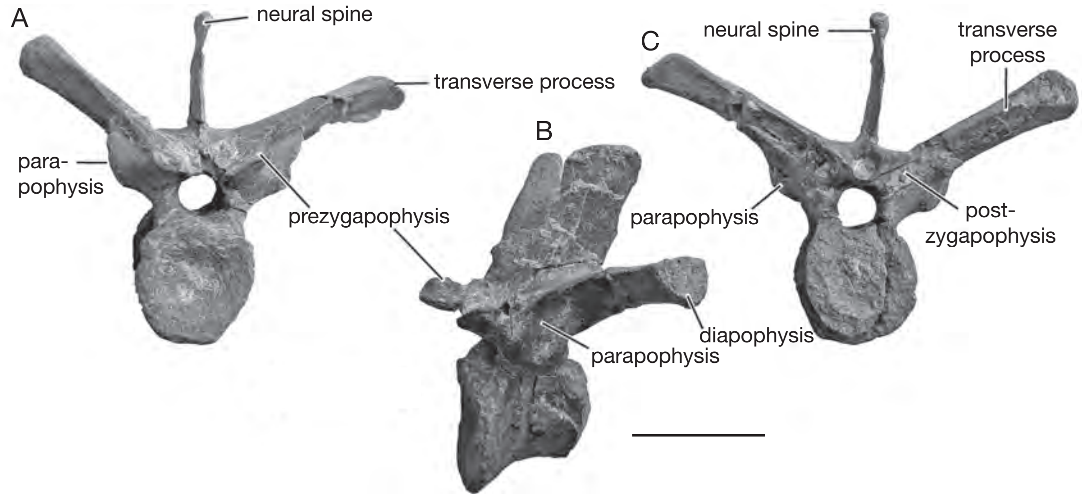

Fig. 12. — Dorsal vertebra (UBB NVZ1-5) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in anterior (**A**), left lateral (**B**), and posterior (**C**) views. Scale bar: 4 cm.

and 75° to the horizontal. The lingual side of the crown is characterized by a strong primary ridge, slightly mesial to the midline of the crown (*contra* Weishampel *et al.* 2003). From eight to 13 slightly divergent vertical subsidiary ridges cover either side of the median ridge (Fig. 11A). The mesial edge of the crown bears tiny crenulations. There is no real cingulum, but a thin enamelled lip marks the base of the distal part of the crown. The root is somewhat higher than the crown and regularly curved labially. Grooves on either side of the root and at the base of the crown indicate that the teeth were closely packed (Fig. 11C).

Dorsal vertebrae (Fig. 12) (UBB NVZ1-3, NVZ1-4, NVZ1-5, NVZ1-6, NVZ1-7, NVZ1-12, NVZ1-13, NVZ1-15, NVZ-7)

The centrum of the dorsal is approximately as long as high, usually very contracted between the articular surfaces and keeled along its ventral surface. The centrum of more posterior dorsal vertebrae becomes larger, the lateral sides become more contracted and the ventral keel becomes more rounded. The articular surfaces are slightly amphicoelous to amphiplatyan. The anterior surface is usually larger than the posterior surface. In lateral view, the planes formed by the anterior and posterior articular surfaces converge ventrally and the ventral border of the centrum has consequently an arched aspect (Fig. 12B). The prezygapophyses face dorsally and medially. They are better separated from each other on the most anterior vertebrae. On the most anterior vertebrae of the preserved series, the transverse processes are oriented posterodorsally; posteriorly in the dorsal series, the transverse processes become straighter, more horizontal and stouter. The postzygapophyses face ventrally and laterally. They increase in size and curvature posteriorly. In lateral view, the neural spine is approximately as high as the centrum and sub-rectangular in shape. It is more inclined posteriorly on the anterior than on the most posterior dorsal vertebrae of the preserved series.

Sacrum (Fig. 13) (UBB NVZ1-9, NVZ1-10, NVZ1-11, UBB SPZ-2)

UBB SPZ-2 has already been briefly described and figured by Weishampel *et al.* (2003). However, it appears that there are some minor misinterpretations in their description. Moreover, the preparation of this specimen has been completed in the meantime. Therefore, it has been decided to include this material in the description of *Z. shqiperorum*. Despite its fusion to the sacrum, the first vertebra of the series can be interpreted as the last dorsal vertebra.

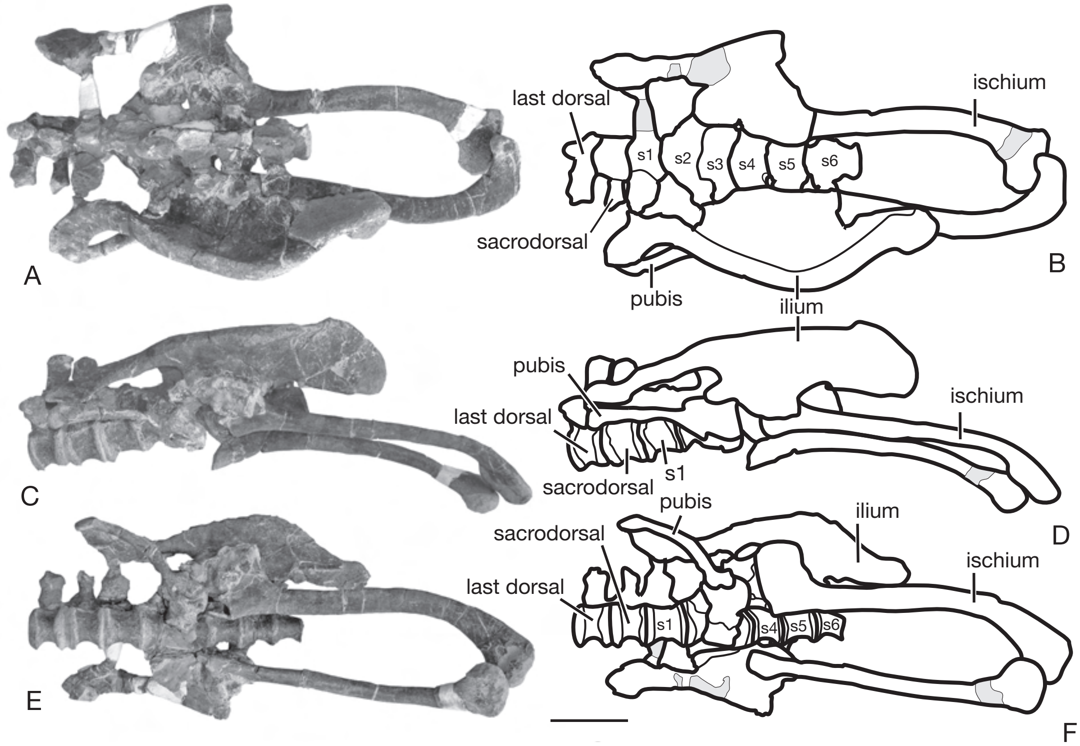

FIG. 13. — Articulated sacrum, ilia, ischia, and left pubis (UBB SPZ-2) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in dorsal (**A**, **B**), left lateral (**C**, **D**), and ventral (**E**, **F**) views. Scale bar: 10 cm.

Its centrum is sub-circular in cross-section and its lateral sides are strongly contracted. In lateral view, its articular surfaces slightly converge ventrally. The ventral keel is very rounded on its centrum. Its transverse processes are stout. Its neural spine is rectangular, with a thickened upper edge, and is slightly inclined posteriorly.

The second vertebra of the series is somewhat larger than the first, but it is very similar in shape. However, it can be regarded as a sacrodorsal vertebra instead of a dorsal vertebra, because the rib of the succeeding first true sacral vertebra has migrated anteriorly to fuse across the articulation between both adjacent vertebrae. This first sacral rib is directly connected to the medial side of the preacetabular process of the ilium and does not participate in the sacrocostal yoke. The rib of the sacrodorsal vertebra is not preserved, but it may have been attached to the medial surface of the preacetabular process of the ilium as well.

There are six firmly co-ossified true sacral vertebrae. The centrum of the first one is particularly massive, with a posterior articular surface much larger than the anterior surface. The centra of the following vertebrae progressively become narrower. The ventral part of the sacral centra forms a shallow continuous groove, well visible on UBB NVZ1-9 and NVZ1-11. At the junction between adjacent vertebrae, five massive sacral ribs are fused together to form a broad sacrocostal yoke, which attaches to the internal surface of the ilium in the region spanning the acetabulum. The neural arches of the sacral vertebrae slightly overlap the centrum of the preceding vertebra. The prezygapophyses are very elongated to fit with the postzygapophyses of the preceding sacral vertebra. The neural spines of the

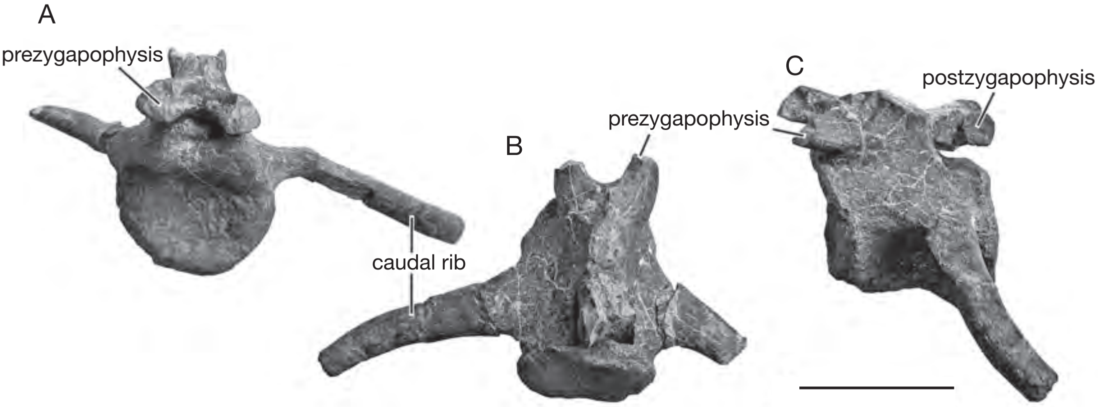

FIG. 14. — Caudal vertebra (UBB NVZ1-14) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in anterior (**A**), dorsal (**B**), and left lateral (**C**) views. Scale bar: 4 cm.

sacrals are not well preserved, but they were low, rectangular in lateral view, and their thickened upper edges were at least partially fused together.

Caudal vertebrae (Fig. 14) (UBB NVZ1-8, NVZ1-14, NVZ-8, NVZ-15, NVZ-16)

The articular surfaces of the caudal vertebrae of *Z. shqiperorum* are slightly amphicoelous and nearly as wide as high. In lateral view, the proximal and distal articular surfaces are sub-parallel and inclined posteriorly. The distal articular surface is higher than the proximal surface and the ventral margin, between both articular surfaces, is strongly concave. The haemapophyseal facets are more distinct on the ventral surface of UBB NVZ1-8 than in the more proximal vertebrae. A pair of longitudinal ridges joins the haemapophyseal facets and the ventral surface of the centrum looks consequently furrowed. The slender caudal ribs are fused to the sides of the centra along the neurocentral suture. The pre- and postzygapophyseal processes become more elongated as the size of the neural arch diminishes and as the centrum becomes proportionally more elongated, and the zygapophyseal surfaces become nearly vertical.

Scapula (Fig. 15A-C) (UBB NVZ1-21, NVZ1-24, NVZ2-2)

As previously described by Weishampel *et al.* (2003), the scapula of *Z. shqiperorum* is markedly different from that of *Z. robustus*. The shaft of the scapular blade is very narrow and strap-like. Its posterodorsal end sharply expands posteriorly. The ventral end of the scapula is also much expanded. The anteroventral acromial region is flared and its lateral surface bears a strong deltoid ridge, which limits a vast deltoid fossa (Fig. 15A). Both the sutural surface for the coracoid and the glenoid part of the scapula are thick, moderately concave and very rugose.

Coracoid (Fig. 15D, E) (UBB NVZ1)

The coracoid is characterized by its unusually long and prominent posterior sternal process, as previously described by Weishampel *et al.* (2003). The glenoid facet is reniform and concave at its centre. The glenoid facet forms a prominent lip on the lateral surface of the coracoid. The coracoid foramen perforates the thickest part of the bone, beneath the scapulocoracoid suture.

Humerus (Fig. 16) (UBB NVZ2-3, NVZ2-4, NVZ-5)

The humerus of *Z. shqiperorum* differs from that of *Z. robustus* by the important development of its deltopectoral crest, which extends over the proximal end of the humerus. The edge of the deltopectoral crest is regularly concave and turned medially, and its distal tip is very salient. The deltopectoral crest therefore limits a wide bicipital sulcus on the

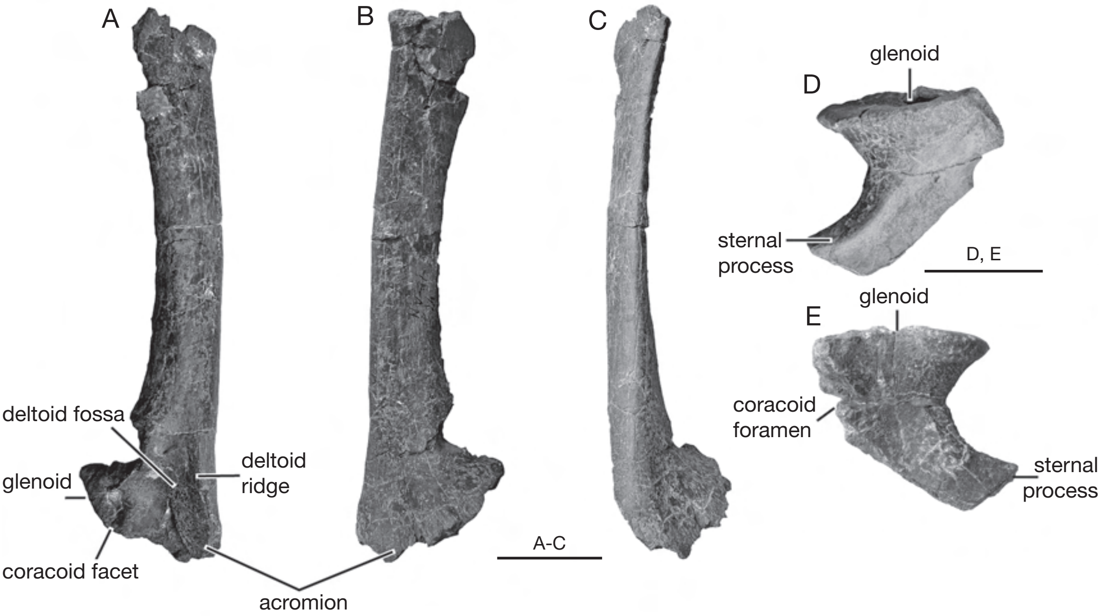

FIG. 15. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), right scapula (UBB NVZ1-24) in lateral (**A**), medial (**B**), and dorsal (**C**) views; left coracoid (NVZ1-36) in medial (**D**) and lateral (**E**) views. Scale bars: A-C, 5 cm; D, E, 4 cm.

anterior surface of the humerus (Fig. 16A). The globular proximal articular head forms a rounded buttress on the posterior side of the humerus. The inner tuberosity is well developed and forms a buttress beneath the concave medial border of the humerus (Fig. 16D). Because of the important development of the deltopectoral crest and of the distal portion of the humerus, the humeral shaft looks proportionally slender. The distal portion of the humerus is mediolaterally expanded and somewhat offset medially. The ulnar condyle is much larger and extends more distally than the radial condyle. The olecranon fossa forms a broad triangular depressed area on the posterior surface of the humerus (Fig. 16B). The coronoid fossa is poorly developed (Fig. 16A).

Ulna (Fig. 17) (UBB NVZ-23)
The ulna of *Z. shqiperorum* is very robust and slightly curved medially. The olecranon process is prominent, but short and blunt. The proximomedial coronoid process is developed into a prominent triangular crest that progressively merges with the ulnar shaft. On the proximodorsal surface of the ulna, the articular facet for the proximal part of the radius is large, triangular in shape and concave. The ulna progressively tapers distally. Its distal end is mediolaterally compressed.

Ilium (Figs 13; 18A-D) (UBB NVZ1-16, NVZ1-17, UBB SPZ-2)
The ilium of *Z. shqiperorum* is particularly massive in dorsal view, because the lateral side of the iliac body faces dorsomedially, forming an angle of about 30° to the horizontal plane. Moreover, the dorsal edge of the ilium is sigmoidal and particularly thick (Fig. 18A). It is ornamented by numerous longitudinal ridges, indicating that it served as attachment site for a strong pelvic musculature (see e.g., Galton 1974 and Norman 1986, for a detailed description of the musculature of the pelvic girdle and hind limb in ornithopods). The preacetabular process is long and dorsoventrally flattened. It is curved laterally and its dorsal surface slightly faces

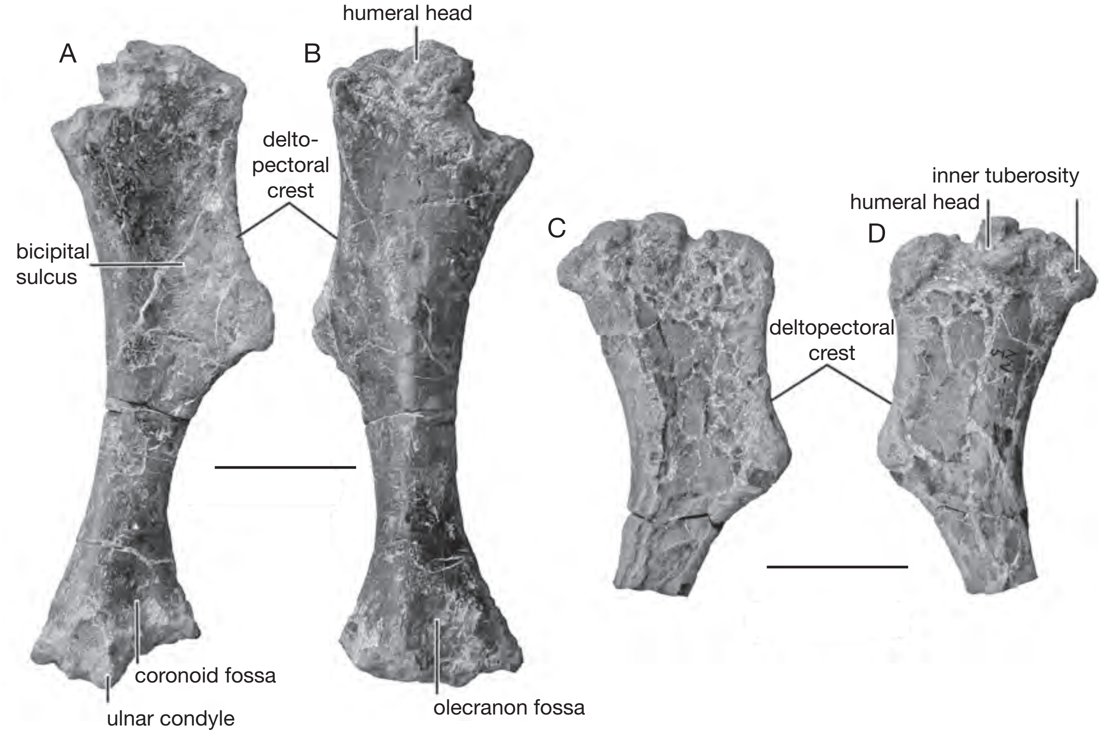

FIG. 16. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), left humerus (UBB NVZ4) in anterior (**A**) and posterior (**B**) views; left humerus (UBB NVZ5) in anterior (**C**) and posterior (**D**) views. Scale bars: 5 cm.

laterally. A prominent longitudinal groove, limited dorsally by a high and sharp ridge, runs along its medial surface (Fig. 18B). The preacetabular notch is very deep. Above the acetabulum, the body of the ilium is lower than in *Z. robustus*. The morphology of the acetabulum is fundamentally different between both species. In *Z. robustus*, the acetabulum is of limited extend, forming a shallow breach between the enormous, lenticular ischial peduncle and the smaller pubic peduncle. In *Z. shqiperorum*, on the other hand, the pubic peduncle is better developed, extending below the level of the ischial peduncle, and the acetabulum forms a well-developed and regularly concave embayment on the ventral part of the ilium (Fig. 18A). The acetabular surface is limited laterally, from the most anterior point of the ischial penduncle to the tip of the pubic peduncle, by a continuous ridge. Above and posteriorly to the acetabulum, the dorsal margin of the ilium is everted to form a prominent supra-acetabular shelf (Fig. 18A), much more developed than in *Z. robustus*. The postacetabular process is long and robust. Its dorsal margin much more everted laterally than in *Z. robustus*, in continuity with the supra-acetabular shelf.

Ischium (Figs 13; 18E, F) (UBB NVZ1-18, NVZ1-21, NVZ1-22, UBB SPZ-2)

The iliac peduncle is much more developed in *Z. shqiperorum* than in *Z. robustus* and forms a slightly depressed elliptical surface that fits the globular ischial peduncle of the ilium. The pubic peduncle is more slender and elongate. Between the iliac and pubic peduncles, a shallow embayment forms the posteroventral margin of the acetabulum. The ischial shaft is mediolaterally flattened. Its distal half is curved ventrally. The distal end of the ischium is curved laterally and forms a prominent boot-like expansion. Its medial side is flat and bears numerous striations, indicating a strong ligamentous attachment with the paired element. Like in *Z. robustus*, there is no obturator process on the ischial shaft.

Pubis (Fig. 13) (UBB SPZ-2)
Both the iliac and the ischial peduncles are wide and cup-shaped. The small embayment between them forms the anteroventral margin of the acetabulum. There is apparently no pubic foramen. The prepubic neck is long and very slender. The prepubis is also very slender and only slightly expanded dorsally.

Femur (Fig. 19) (UBB NVZ1-25, NVZ-1, NVZ2-5, NVZ2-6, NVZ-9, NVZ-21)
The femur of *Z. shqiperorum* closely resembles that of *Z. robustus* in being distinctly bowed laterally in anterior view and nearly straight in lateral view. The femoral head is massive and hemispherical. It is set off from the long axis of the shaft by a relatively long neck. The greater trochanter is regularly rounded and is somewhat lower than the femoral head. The anterior trochanter is apparently better developed than in *Z. robustus*, particularly in larger specimens. It is separated from the greater trochanter by a vertical cleft. Its external surface bears strong striations, marking the insertion area for a powerful *m. ilio-femoralis externus*. The lateral side of the greater trochanter forms an extended depressed area, limited anteriorly by the anterior trochanter, and posteriorly and ventrally, by a strong but smooth ridge (Fig. 19D). Its striated surface served as attachment site for a very powerful *m. ilio-trochantericus*. The pendant fourth trochanter is placed at the mid-shaft. The medial condyle is stouter, but the lateral condyle extends further distally. The flexor intercondylar groove is much deeper and wider than the extensor intercondylar groove. The posterolateral surface of the lateral condyle forms a long but shallow vertical groove for *m. iliofibularis* (Fig. 19D).

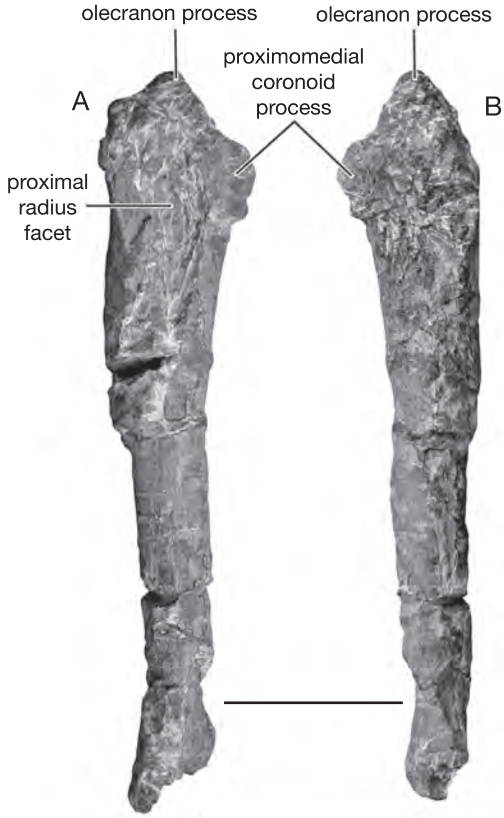

FIG. 17. — Right ulna (UBB NVZ23) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in anterior (**A**) and medial (**B**) views. Scale bar: 5 cm.

Tibia (Fig. 20A-D) (UBB NVZ-2, NVZ-3)
The tibia is less massive in *Z. shqiperorum* than in *Z. robustus*. Its posteroproximal angle forms a prominent internal condyle that overhangs the tibial shaft. It is separated by a shallow popliteal groove from the smaller lateral condyle. The cnemial crest is less prominent than in *Z. robustus* and more derived ornithopods, and occupies only about the proximal fifth of the tibia. Its anteroproximal surface forms a deep and wide anterior groove, probably marking the attachment area for the strong distal ligament of *m. ilio-tibialis* (Fig. 20B). This groove has not been described in *Z. robustus* (Weishampel *et al.* 2003). The tibial shaft is long, more slender than in *Z. robustus*, and ovoid in cross-section. In anterior view, it is less bowed laterally than in *Z. robustus*. Below the end of the cnemial crest, a round vertical ridge descends to the lateral edge

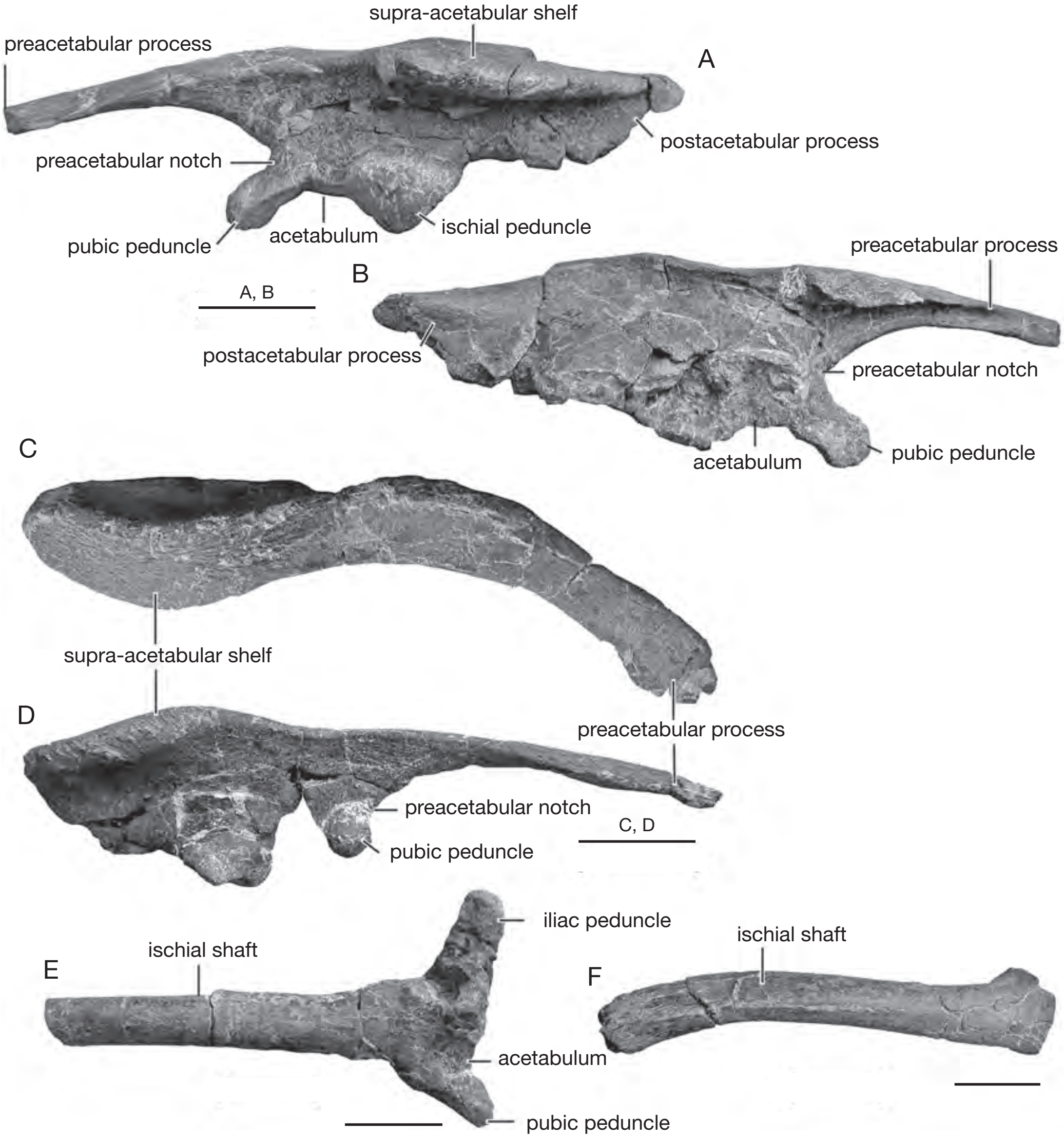

FIG. 18. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), left ilium (UBB NVZ1-17) in lateral (**A**) and medial (**B**) views; right ilium (UBB NVZ1-16) in dorsal (**C**) and lateral (**D**) views; right ischium (UBB NVZ1-22) in lateral view (**E**); left ischium (UBB NVZ1-18) in medial view (**F**). Scale bars: 5 cm.

of the lateral malleolus. On the distal end of the tibia, the external malleolus is very salient distally. The internal malleolus is, on the other hand, more salient medially, with an articular surface turned towards the anterolateral side of the tibia.

Fibula (Fig. 20E, F) (UBB NVZ1-28)

Like in *Z. robustus*, the fibula of *Z. shqiperorum* is slender. The medial surface of the proximal half of the shaft forms a concave surface that is irregularly bordered by smooth anterior and posterior ridges.

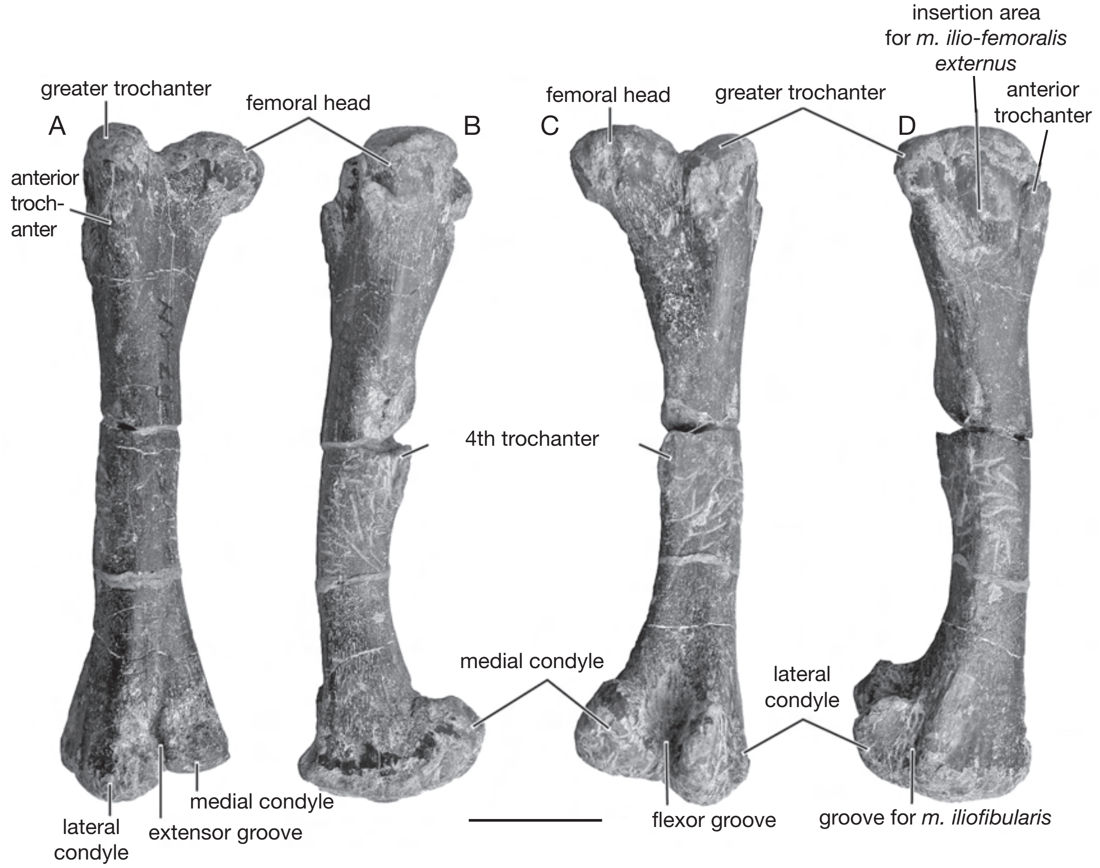

FIG. 19. — Right femur (UBB NVZ9) of *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), in anterior (**A**), medial (**B**), posterior (**C**), and lateral (**D**) views. Scale bar: 5 cm.

This surface is also ornamented by longitudinal ridges, indicating that it was firmly attached to the tibial shaft by ligaments.

Metatarsals

Metatarsal II of *Z. shqiperorum* (UBB NVZ1-30; Fig. 20G, H) is elongated and rather slender. Its proximal end is mediolaterally compressed and plantodorsally expanded. Its medial surface bears strong longitudinal striations, indicating ligamentous attachment with metatarsal I. Its lateral side forms a flat triangular surface that also bears longitudinal striations marking strong attachment to metatarsal III. The distal end of metatarsal II is plantodorsally expanded and only a little wider than the distal end. Its medial side is smoothly convex, whereas its lateral side is flat. The distal articular surface is regularly convex and it slightly faces medially. A shallow intercondylar groove is developed on its plantar aspect and probably acted as a pulley to guide a powerful flexor tendon.

Only the distal portion of metatarsal III (UBB NVZ1-34; Fig. 20I, J) is preserved. It is rather slender too, with a trapezoidal dorsoplantarly flattened shaft, whose medial side is higher than its lateral side. The distal end of metatarsal III is expanded into a large saddle-shaped and dorsoplantarly convex articular surface. The intercondylar groove is well developed both on the dorsal and plantar parts on the condyle. The medial condyle is more developed than the lateral condyle. Both the medial and lateral sides of the distal articular end form cup-like depressions.

SYSTEMATIC OBSERVATIONS

Weishampel *et al.* (2003) based their description of *Z. shqiperorum* mainly on postcranial material, collected in various localities in the Haţeg Basin. Of the cranial material, only the dentary of *Z. shqiperorum* was known at that time. The discovery at Nălaţ-Vad of fairly well-preserved skull material, in association with postcranial elements, is therefore important for a better understanding of this species and, more generally, of *Zalmoxes*. Indeed, in their diagnosis of *Zalmoxes*, Weishampel *et al.* (2003) listed a number of characters that were in fact not known in the material pertaining to *Z. shqiperorum* or in the different species of *Rhabdodon*. Consequently it was in fact impossible to decide whether these characters were really synapomorphic for *Zalmoxes*, synapomorphic for Rhabdodontidae, or autapomorphic for *Z. robustus*. The study of the Nălaţ-Vad material confirms that the following characters can be observed in both *Z. robustus* and *Z. shqiperorum*:

1. extensive, complex squamose suture between quadratojugal and jugal;
2. post-temporal foramen transmitted through the body of the squamosal;
3. curved shelf on the lateral surface of the postorbital;
4. lateral splaying of the quadrate;
5. deep predentary;
6. long, dorsoventrally-narrow, twisted preacetabular process;
7. absence of an obturator process on the ischium;
8. arched ischial shaft.

Nevertheless, only the last two characters can be regarded as strictly synapomorphic for *Zalmoxes*. Indeed, the state of the other features remains unknown in *Rhabdodon* and it cannot therefore be excluded that they represent in fact synapomorphies for Rhabdodontidae.

Weishampel *et al.* (2003) regarded the presence of a well-developed supra-acetabular process on the ilium as an autapomorphy for *Z. robustus*. However, re-examination of UBB SPZ-2 and discovery of new material at Nălaţ-Vad reveal that the supra-acetabular process is well developed in *Z. shqiperorum* as well. On the other hand, it is apparently not developed in *R. priscus* (Pincemaille-Quillévéré 2002: fig. 15) and other basal Iguanodontia (Norman 2004). Therefore, a well-developed supra-acetabular process can be regarded as a diagnostic character for *Zalmoxes*.

Weishampel *et al.* (2003) considered that a reduced external mandibular fenestra, positioned along the upper anterior border of the surangular and overlapped by the dentary, and the development of a secondary surangular foramen are also synapomorphic for *Zalmoxes*. The description of the material from Nălaţ-Vad confirms that *Z. shqiperorum* is characterized, like *Z. robustus*, by a reduced external mandibular fenestra (the posterior part of the surangular, with the secondary foramen, is not preserved). However, Pincemaille-Quillévéré (2002) also describes two foramina on the external surface of the surangular in *R. priscus*. It is therefore quite possible that those foramina respectively represent a reduced external mandibular fenestra and a secondary mandibular foramen. In this case, both characters would represent synapomorphies for the Rhabdodontidae clade. In any case, the reduced external mandibular fenestra is placed more anteriorly in *Z. robustus* and *Z. shqiperorum* than the anterior foramen on the surangular of *R. priscus*.

The following characters, regarded as diagnostic for *Zalmoxes* by Weishampel *et al.* (2003), cannot be observed either in *Z. shqiperorum* or in the different species of *Rhabdodon*; therefore, subsequent discoveries may shift their distribution either inclusively (as synapomorphies for the Rhabdodontidae clade) or exclusively (as autapomorphies for *Z. robustus*):

1. absence of the scar for *m. adductor mandibulae externus superficialis* on the squamosal;
2. a large, disc-shaped quadratojugal;
3. a frontal with a complex transverse sutural surface that extensively overlaps the parietal;
4. high lateroventral processes on the predentary.

The following characters appear autapomorphic for *Z. shqiperorum*. Indeed, they have not been observed either in *Z. robustus* or in other basal Iguanodontia:

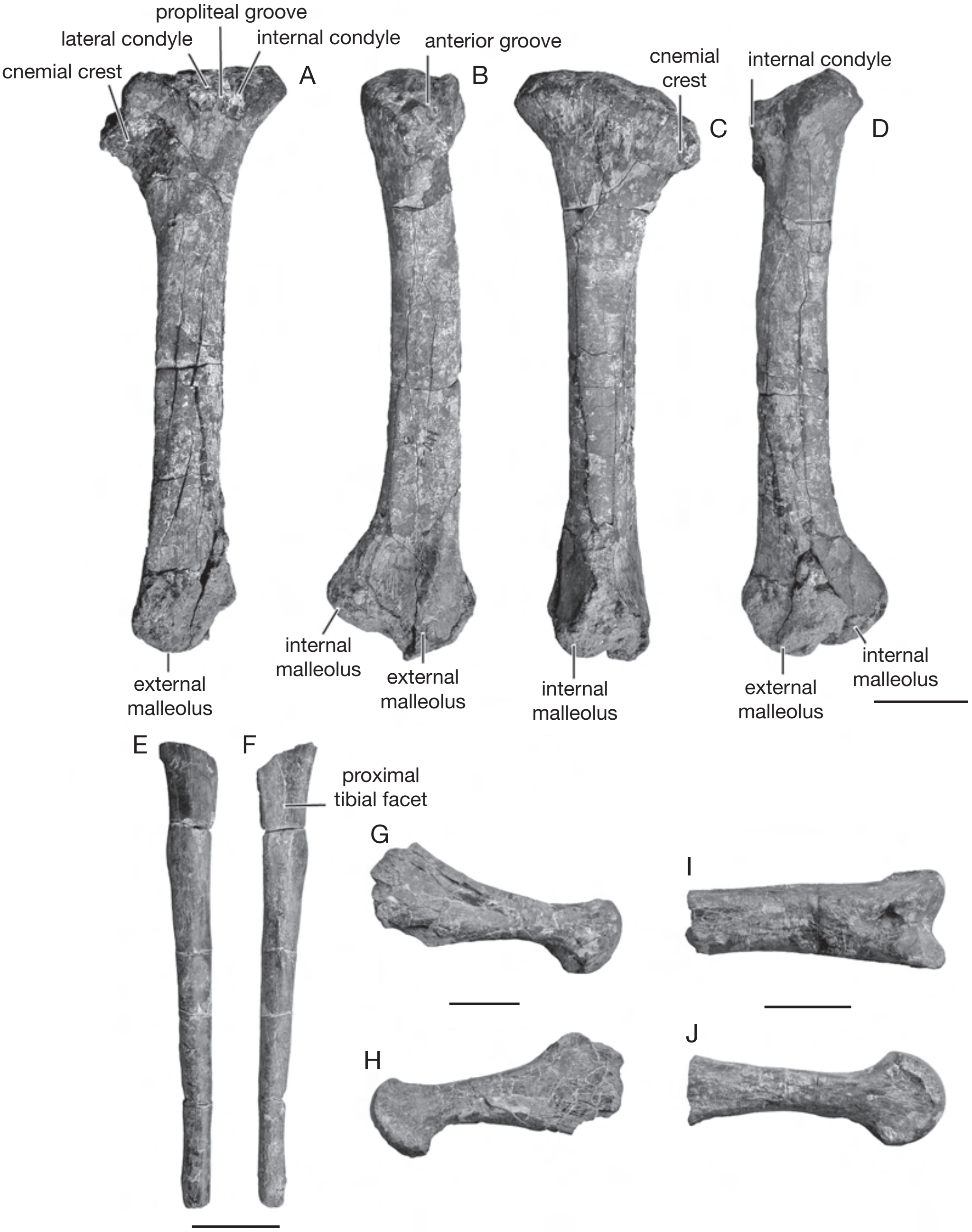

Fig. 20. — *Zalmoxes shqiperorum* Weishampel, Jianu, Cziki & Norman, 2003 from the Upper Cretaceous of Nălaţ-Vad (Romania), left tibia (UBB NVZ3) in lateral (**A**), anterior (**B**), medial (**C**), and posterior (**D**) views; ?left fibula (UBB NVZ1-28) in lateral (**E**) and medial (**F**) views; left metatarsal II (UBB NVZ1-30) in medial (**G**) and lateral (**H**) views; ?left metatarsal III (UBB NVZ1-34) in plantar (**I**) and ?medial (**J**) views. Scale bars: A-D, 5 cm; E, F, 4 cm; G-J, 3 cm.

1. the occipital condyle is not separated from the sphenooccipital tubercles by a distinct neck;
2. the dentary bears an angular buccal emargination that forms a horizontal platform extending for the full length of the dentition behind and medial to the coronoid process (Weishampel *et al.* 2003);
3. the scapular blade is narrow and strap-like proximally and expands sharply posterodistally (Weishampel *et al.* 2003);
4. the region of the scapula adjacent to the coracoid suture is expanded; acromial process forming a prominent flange (Weishampel *et al.* 2003);
5. the deltopectoral crest of the humerus is particularly prominent, extending over the proximal half of the humerus;
6. the iliac peduncle of the ischium is particularly developed;
7. the distal end of the ischium forms a boot-like expansion (Weishampel *et al.* 2003).

The description of the Nălaţ-Vad material reveals that *Z. shqiperorum* potentially differs from *Z. robustus* by a series of other characters, listed below. However, these characters cannot be adequately quantified in the current state of our knowledge, because we lack more precise information about their intraspecific variability. Moreover, their state remains ambiguous:

1. the jugal appears more gracile in *Z. shqiperorum*;
2. the parietal process of the squamosal is apparently shorter, but higher;
3. the infratemporal notch on the squamosal appears lower, but deeper;
4. the post-temporal foramen is set more anteriorly;
5. the sagittal crest is better developed;
6. the dentary is more massively constructed;
7. the oral margin of the predentary is apparently characterized by a sharper outer margin;
8. the anterior trochanter is better developed on the femur;
9. the tibia appears less massive.

SYMPATRIC SPECIES IN ORNITHOPODS

The observed morphological differences between *Z. robustus* and *Z. shqiperorum* appear, in any case, sufficient to support the validity of both species. There is no indication that these differences reflect ontogenetic variability within a single species: smaller and larger individuals are clearly represented in both groups. The differences between *Z. robustus* and *Z. shqiperorum* also appear too important to simply reflect sexual dimorphism. As observed in lambeosaurines (Dodson 1975), in basal neceratopsians (Dodson 1976), or in ceratopsids (Lehman 1990; Sampson *et al.* 1997), dinosaur males and females may not be distinguished by the presence or absence of osteological characters, but instead by the difference in development of cranial superstructures (crests, horns, frills) at a given size. It is now usually admitted that these structures primarily functioned as signals to recognize and to compete for mate or territory. Such characters are subject to delayed growth, developing only after the onset of adult size (Dodson 1975; Sampson *et al.* 1997). Sexual dimorphism in the postcranial skeleton has not been well studied yet. However, Raath (1990) tentatively explained the morphological variation in the robustness of the postcranial skeleton of the basal theropod *Syntarsus* by sexual dimorphism: he suggested that the most robust morph might represent females. In *Zalmoxes*, important differences in the skull element and in the postcranium between the two supposed species are not simple variations in the development of supracranial structures or in the robustness of the bones, but true osteological. For examples, it seems difficult to explain the observed differences in the morphology of the basioccipital, the scapula or the ischium by sexual dimorphism: these characters cannot be recognized as visual signals. Moreover, these features were apparently already developed in juveniles, before individuals have reached sexual maturity.

Figure 1 represents the geographic distribution of *Z. robustus* and *Z. shqiperorum*. Both species have been discovered together in several localities (Sănpetru, Tustea, Valioara, Vurpar) and, so far, there is no indication that they were found in different levels. Although they clearly occupied very similar ecological niches and probably competed for the same food resources, the two species therefore appear sympatric. As discussed below, it is not the first time that two closely-related species of an ornithopod genus are described in a same locality and are therefore regarded as sympatric.

At Bernissart (Belgium, Early Cretaceous), two or three specimens of the gracile species *Iguanodon atherfieldensis* Hooley, 1925 have been discovered together with more than 20 specimens of the robust *I. bernissartensis* Boulenger, 1881 (Norman 1986). Paul (2007) proposed that *I. bernissartensis* and *I. atherfieldensis* do not form a monophyletic group and that morphological differences are sufficient to include the latter species into a separate genus, *Mantellisaurus* Paul, 2007. However, he conducted no phylogenetic analysis proving that *I. bernissartensis* and *I. atherfieldensis* are really paraphyletic. On the other hand, in the most recent phylogenetic analysis of the group, Norman (2004: fig. 19.22) suggested that both species may be regarded as monophyletic and, if this hypothesis is correct, it is certainly not necessary to split them into different genera. In any case, it is definitely not proved that *I. bernissartensis* and *I. atherfieldensis* really lived together in the Bernissart area. Indeed, the Bernissart fossil locality is apparently an attritional accumulation of animals dead in different places and at different times. During Early Cretaceous times, the Bernissart site may have been somewhat lower topographically than the surrounding countryside because of subterranean dissolution, which should explain the preferential accumulation of fossils at Bernissart (Delmer & Van Wichelen 1980). However, these two species have also been described together in many other Early Cretaceous formations from Western Europe, suggesting that they were really sympatric in this area. Although the holotype of *I. atherfieldensis* Hooley, 1825 (BMNH R5764) was collected from the Vectis Formation, most of the *Iguanodon* specimens collected in the south-west coast of the Isle of Wight, including partial skeletons and isolated bones of both *I. atherfieldensis* and *I. bernissartensis*, were found in different points of the underlying Wessex Formation (Martill & Naish 2001). The Smokejacks Pit locality (Surrey, UK) has also yielded good material belonging to both *I. atherfieldensis* and *I. bernissartensis* (Benton & Spencer 1995). Both species were also reported from the Hastings Beds and Weald Clay of West Sussex, with *I. anglicus* Holl, 1829 (regarded as valid by Norman & Weishampel [1990] and Norman [2004]), in the Tilgate Forest area, the historical place where the first dinosaur specimens were discovered in the 19th Century (Benton & Spencer 1995; Weishampel *et al.* 2004). Unfortunately, because the quarries have been closed for a long time, most of the discovery sites remain uncertain. The Hastings Beds (Berriasian-Vallanginian) that outcrop along the coast east of Hastings (East Sussex, United Kingdom) are also famous for their vertebrate remains. Three Iguanodon species have been described from this area: *I. dawsoni* Lydekker, 1888 and *I. fittoni* Lydekker, 1889, from Shorden Quarry, and *I. hollingtonensis* Lydekker, 1889, from Hollington Quarry. Norman & Weishampel (1990) and Norman (2004) synonymised *I. hollingtonensis* with *I. fittoni* and accepted *I. dawsoni* as valid, but do not elucidate the differences of these poorly known taxa from the typical *I. bernissartensis* and *I. atherfieldensis*. In France, Iguanodon specimens were found in Early Cretaceous deposits from the Saint-Dizier region (Haute-Marne). However, the two species were found in different localities: *I. bernissartensis* at Baudonvilliers, Pont-Varin and Saint-Dizier, and *I. atherfieldensis* at Wassy and Coursancelles (Martin & Buffetaut 1992; É. Buffetaut pers. comm. 2006). Adult and numerous juvenile remains of both *I. atherfieldensis* and *I. bernissartensis* were discovered in a cavern-like deposit at a quarry near the village of Nehden in Sauerland (Germany). Contrary to the Bernissart assemblage, the Nehden fauna is dominated by *I. atherfieldensis* specimens and by juveniles. According to Norman (1987) and Norman *et al.* (1987), the assemblage at Nehden may represent a catastrophic accumulation caused by a flash flood or by a herd crossing a river. However, the over-representation of juvenile specimens in a fossil assemblage is a good indicator for an attritional death profile (Lyman 1994): the observed peaks corresponding to ages where mortality rates are the highest, among the very young and, to a lesser extent, the very old. Therefore, it cannot be excluded that the Nehden assemblage represents, like Bernissart, an allochtonous accumulation of animals dead in different places and times. Fragmentary remains identified as *I. bernissartensis* and *I. atherfieldensis* ("*I. mantelli*") have been described together in the Camarillas Formation (Barremian) of the San Cristobal and Santa Barbara localities (Teruel Province, Spain; Sanz *et al.* 1984a, b). However, the described material appears poorly diagnosed and the identification is mainly based on the size of the bones. Moreover, Ruiz-Omeñaca & Canudo (2004) consider that the material from Teruel Province previously referred to as *I. bernissartensis* would in fact belong to a new iguanodontian genus. In conclusion, the distribution of the different *Iguanodon* species clearly shows the difficulty to decide whether the presence of two species within a same formation results from the sympatry of these species or from taphonomic processes.

The famous Quarry 13 in the Morrison Formation near Como (Wyoming) has yielded the holotypes of four *Camptosaurus* Marsh, 1885 species: *C. dispar* (Marsh, 1879), *C. medius* Marsh, 1894, *C. nanus* Marsh, 1894 and *C. browni* Gilmore, 1909. Norman & Weishampel (1990), and Norman (2004) considered these taxa as synonyms, but regarded *C. amplus* (Marsh, 1879), from the neighbouring Quarry 1A at Como Bluff, as a valid species. However, this latter taxon is based on a pes, which closely resembles that of theropod dinosaurs.

The Dinosaur Park Formation of Alberta (Canada) has yielded at least eight valid hadrosaurid species (Ryan & Evans 2004), including two valid species of *Lambeosaurus* Parks, 1923 (*L. lambei* Parks, 1923 and *L. magnicristatus* Sternberg, 1935) and two species referred to *Gryposaurus* Lambe, 1914 (*G. notabilis* Lambe, 1914 and *G. incurvimanus* Parks, 1920). Recent data on the stratigraphic position of articulated and associated skeletons within the Dinosaur Park Formation indicate that *Lambeosaurus magnicristatus* has no stratigraphic overlap with *L. lambei* and suggests that it replaces *L. lambei* on a regional scale in southern Alberta (Evans & Reisz 2007). Currie & Russell (2004) also indicate that all *Gryposaurus incurvimanus* specimens are higher in the Dinosaur Park Formation than specimens of *G. notabilis*.

Two species are also currently recognized within *Rhabdodon*, the sister-taxon of *Zalmoxes*. *Rhabdodon priscus* is recorded in various formations and localities from Aude, Hérault, Bouches-du-Rhônes, Var, Ariège and Gard in Southern France. *Rhabdodon septimanicus* is currently known by a single right dentary, from the “Grès à Reptiles” formation in Montouliers (Hérault). Two species of *Rhabdodon* therefore apparently coexist in the “Grès à Reptiles” formation of the Saint-Chinian area in Hérault. Although *R. septimanicus* was doubted by some authors (Allain & Pereda-Suberbiola 2003), it was accepted by Weishampel *et al.* (2003) and Norman (2004). In any case, Buffetaut (2005) indicated that the abundant *Rhabdodon* material from the Saint-Chinian area apparently includes both a robust and a gracile form. A detailed study of *Rhabdodon* material is currently in progress, which should provide a final answer to the question of how many species of *Rhabdodon* are present in the Late Cretaceous of southern France (É. Buffetaut and P. Chanthasit pers. comm. November 2006).

CONCLUSIONS

The new fossils discovered in the Sănpetru Formation at Nălaţ-Vad include the most complete skeleton that can be referred to date to *Zalmoxes shqiperorum*. The observed morphological differences between *Z. robustus* and *Z. shqiperorum* cannot be adequately explained by ontogenetic variation or sexual dimorphism. Because *Z. robustus* and *Z. shqiperorum* were discovered together in several localities, their sympatry is therefore a hypothesis that cannot be a priori rejected. The sympatry of closely-related species was apparently not an isolated case among ornithopod dinosaurs, even if it is not always easy to decide whether the presence of species belonging to a same genus within a same locality is the result of true sympatry, of taphonomic processes, or of imprecision in the collecting information.

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